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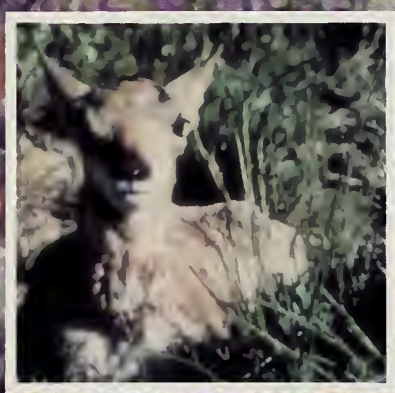


Ecosystem disturbance and wildlife conservation in western grasslands

A symposium proceedings

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Finch, Deborah M., Editor. 1996. Ecosystem disturbance and wildlife conservation in western grasslands — A symposium proceedings. September 22-26, 1994; Albuquerque, NM. General Technical Report RM-GTR-285. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 82 p.

Abstract: This publication is the result of a half-day symposium, "Ecology, management, and sustainability of western grassland ecosystems" held at The Wildlife Society's First Annual Technical Conference, September 22-26, 1994 in Albuquerque, NM. The purpose of the symposium was to review and synthesize information about the structure, function, and components of steppe and desert grassland ecosystems in the western United States with special emphasis on the ecological roles and requirements of wildlife species. This work, designed to draw attention to some wildlife topics that have been particularly neglected for western grasslands, represents a cross-section of the papers orally presented at the symposium as well as some additional papers solicited afterwards. To provide a quality product, a minimum of two peer reviews were solicited for each manuscript, and authors were instructed to revise manuscripts based on editor's and referees' comments. Land managers, range conservationists, wildlife biologists, ecologists, and private citizens interested in sustaining the ecological health, productivity, and biological diversity of western grassland ecosystems should find this publication valuable.

Keywords: steppe and desert grassland ecosystems, wildlife requirements, western grasslands, biological diversity, ecological health

Acknowledgments: The editor thanks Bertie Weddell and Gale Wolters for helping to organize the original symposium session. The Wildlife Society (TWS) hosted the symposium, and the National Biological Service and the U.S. Forest Service, Rocky Mountain Experiment Station co-funded the publication. Appreciation is extended to Norm Scott for assistance in defraying the publication costs; Jim Fenwood for supplying the TWS working group charter; and Bertie Weddell, Chair (1994-95) of the working group, for ideas and inspiration.

Editor's note: Each manuscript received peer review. To deliver symposium proceedings to readers as quickly as possible, manuscripts did not undergo full editing. Views expressed in each paper are those of the author and not necessarily those of the sponsoring organizations or the USDA Forest Service. Trade names are used for the information and convenience of the reader and do not imply endorsement or preferential treatment by the sponsoring organizations or the USDA Forest Service

COVER PHOTOS: Hairy vetch (*Vicia villosa*) blanketing a remnant of original Palouse prairie during a wet year near Pullman, Washington (by John Mitchell, USDA-FS). Insets: Pronghorn antelope (*Antilocapra americana*) fawn, short-grass/sagebrush steppe, southeastern Wyoming (by Deborah Finch, USDA-FS) and Ornate box turtle (*terrapene ornata*), Rita Blanca National Grassland, near Clayton, NM (by Paulette Ford, USDA-FS).

Ecosystem disturbance and wildlife conservation in western grasslands

A symposium proceedings

Editor:

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Sponsors:

The Wildlife Society's Working Group on
Sustainable Use of Ecosystem Resources

The Wildlife Society

National Biological Service, Piedras Bancas Research Station

USDA Forest Service, Rocky Mountain Forest and Range Experiment Station

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Sustaining western grasslands and associated wildlife: An introduction

Deborah M. Finch¹

This publication is the result of a half-day symposium, "Ecology, management, and sustainability of western grassland ecosystems," held at The Wildlife Society's First Annual Technical Conference, September 22-26, 1994 in Albuquerque, NM. The symposium was sponsored by The Wildlife Society's Working Group on Sustainable Use of Ecosystem Resources and was organized by members Deborah Finch, Gale Wolters, and Bertie Weddell. The scope of this working group is the assembly, study, and transfer of information pertaining to the conservation of wildlife through sustainable uses of ecosystem resources throughout the world. Its goals are to facilitate communication and exchange of information among members of The Wildlife Society interested in applying the ecosystem management concept to wildlife conservation; enhance knowledge and technical capabilities of wildlife professionals in the definition, assessment, and implementation of sustainable uses of ecosystem resources; and increase public awareness and appreciation of the effects of resource uses on wildlife and of the role of sustainable resource use in wildlife management. For more information about this working group, see its charter at the end of this volume.

The purpose of the symposium was to review and synthesize information about the structure, function, and components of steppe and desert grassland ecosystems in the western United States with special emphasis on the ecological roles and requirements of wildlife species. Western grasslands under private and agency ownership have traditionally been managed primarily for livestock and crop production. Applied scientific studies have heavily emphasized methods and analyses

aimed at improving plant productivity, increasing livestock weight and numbers, and solving problems that affect economic return. A scientific foundation for maintaining and monitoring populations and communities of grassland wildlife, especially nongame species, in concert with commodity production is not well-established for most grassland ecosystems in western North America. This publication is designed to draw attention to some wildlife topics that have been particularly neglected for western grasslands.

The timing of this publication is especially appropriate because:

1. Scientists are reporting ecosystem endangerment, species endangerment, and animal population declines in many North American grasslands (Finch 1994; Knopf 1994; Flather et al. 1994; Noss et al. 1995; Samson and Knopf 1996);
2. Land-managing agencies with an ecosystem management orientation such as Bureau of Land Management and U.S. Forest Service are showing increasing interest, concern, and emphasis on nontraditional uses for grasslands such as recreation, wildlife viewing, birdwatching, hunting, and fishing (e.g., *Birds of Cimarron National Grassland*, Cable et al. 1996; USDA Forest Service 1996);
3. Professional societies such as the Society of Range Management as well as government and nongovernment organizations are flagging rangeland health and rangeland wildlife as topics of concern (USDA Forest Service, 1992; National Research Council 1994; Krausmann 1996); and
4. Local ranching communities accustomed to using government lands for rearing livestock are expressing uneasiness about tighter permit restrictions and perceived threats to their stockraising traditions and livelihoods.

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Monitoring data and syntheses of existing information are needed to address these shifts in values and resolve conflicting problems.

This publication represents a cross-section of the papers orally presented at the symposium as well as some additional papers solicited afterwards. Each paper was reviewed by a minimum of two peer referees prior to editorial review and publication. The publication begins with a review of climate, phenology, and disturbance factors in steppe and desert ecosystems by Bertie Weddell, followed by an analysis of effects of grazing on grassland ecosystems by Linda Wallace and Mel Dyer. Paulette Ford and Guy McPherson review information on the ecology and role of fire in short-grass prairie, especially in relation to how fire affects vegetation, arthropods, birds, and mammals.

Three papers review the literature on wildlife topics of special interest. Norm Scott provides a comprehensive synthesis of information on the evolutionary ecology and current status of reptiles and amphibians inhabiting North American grasslands. Habitat and roost requirements of bat species using southwestern grasslands are summarized by Alice Chung-MacCoubrey. Deborah Finch and Wang Yong supply an original analysis comparing the population trends, migration, and stopover habitat use of grassland-breeding sparrows to emberizids that breed in other habitats.

The volume ends with a paper by Mike Wolfe highlighting a progressive ecosystem management approach used by an experimental ranch in Utah. Managing for wildlife and livestock production, the ranch successfully demonstrates methods for achieving economic return while maintaining and enhancing land health and biological diversity. In summary, this publication should be of value to land managers, range conservationists, wildlife biologists, ecologists, and private citizens interested in sustaining the ecological health, productivity, and biological diversity of western grassland ecosystems.

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Geographic overview: Climate, phenology, and disturbance regimes in steppe and desert communities

B. J. Weddell¹

Abstract.—In midwestern steppes, precipitation peaks in summer, whereas west of the Rocky Mountains, steppes are characterized by summer drought. In western deserts, the amount of precipitation is highly variable. These different climatic regimes result in differences in prevalence of and resilience to disturbances such as herbivory, and differences in susceptibility to invasion by exotic plants and animals. The timing and predictability of precipitation influences plant phenology and life forms, which in turn influence the distributions and annual cycles of animals such as bison (*Bison bison*) and prairie dogs (*Cynomys* spp.). Desert organisms are susceptible to disturbances that disrupt cues signaling temporarily favorable conditions. Herbivores such as Bay checkerspot butterflies (*Euphydryas editha bayensis*) that are closely tied to the life cycles of their host plants are vulnerable to climatic changes that disrupt this tight phase relationship.

INTRODUCTION

Western rangelands encompass a variety of steppe and desert communities that are too dry to support trees as their dominant vegetation. Although the ecosystems that are considered in this symposium are all similar in this respect, they differ in climate, topography, and floristic history. This geographic overview focuses on differences in climate, because climate influences the magnitude of ecosystem productivity and the timing of that productivity, both of which influence sensitivity to disturbance and to invasion by exotic species.

This review describes the major climate regimes of western grassland ecosystems and presents examples that illustrate how climate, particularly the timing and predictability of precipitation, influences animal distribution and activity cycles. This study concludes with a brief discussion of some possible consequences of rapid climate

change for grassland organisms and a discussion of the implications to sustainability.

The terminology surrounding grassland ecosystems is confusing. The word grassland itself and related words such as desert, desertification, and rangeland are often used without being clearly defined. While I doubt that it is possible to come up with a set of definitions that everyone can agree upon, I hope that this geographic overview will at least reduce some of the confusion surrounding these terms.

MAJOR CLIMATE PATTERNS IN NORTH AMERICAN STEPPE AND DESERT

On the basis of climate, the grassland ecosystems of western North America can be grouped into three major categories: the midwestern steppes east of the Rocky Mountains, the western steppes and shrub steppes west of the Rocky Mountains, and the southwestern and Mexican deserts. Patches of grassland also occur as openings or parks within forested landscapes on soils that are incapable of

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supporting trees and on sites where fire prevents trees from becoming established (Daubenmire 1978).

The approximate distributions of the major units of steppe and desert vegetation of North America are shown in figure 1. The term steppe refers to areas where conditions are too dry for trees and the vegetation is dominated by perennial grasses. The steppes of North America fall into two categories. The midwestern or Great Plains steppes

(figs. 1B, C, D) are located east of the Rocky Mountains and west of the area capable of supporting fire-maintained grassland. The western steppes of the Intermountain West and California's Central Valley (figs. 1E, F, G) occur west of the Rocky Mountains. In parts of this region such as north-central Oregon, central Washington, and southern Idaho, perennial grasses are accompanied by an overstory of shrubs, particularly big sage-

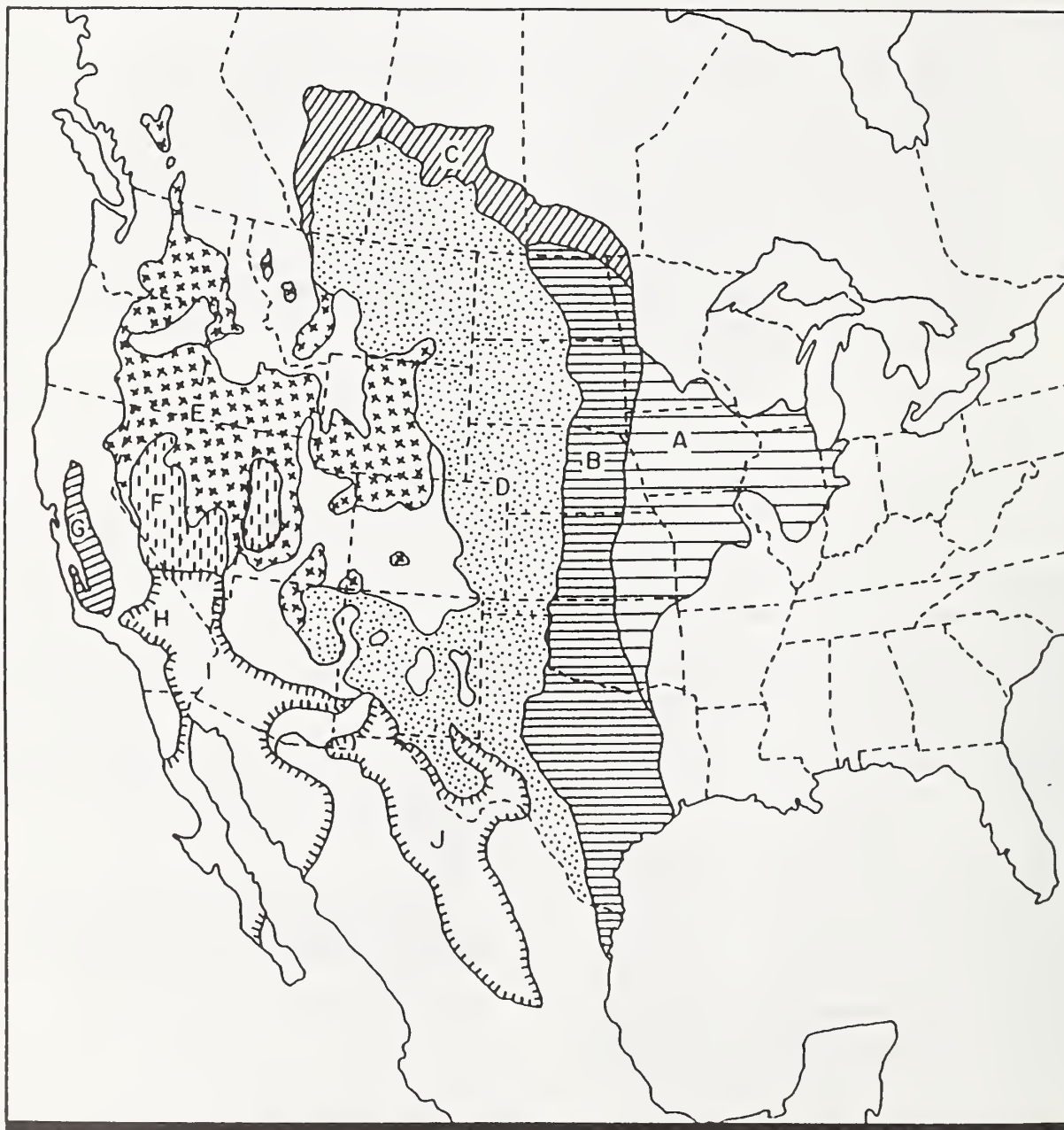


Figure 1. Approximate distribution of major units of steppe and desert vegetation of North America. A) area capable of supporting fire-maintained grassland; B, C, D) Midwestern steppes; E, F, G) western steppes; H, I, J) desert. After Daubenmire, *Plant Geography*, 1978.

brush (*Artemisia tridentata*). This type of community is termed shrub-steppe (Daubenmire 1978).

Desert has been defined in many ways. This review follows Daubenmire (1978) in using the word desert to refer to areas where precipitation is low in relation to heat level, so that the substrate is moist for only brief periods (figs. 2H, I, J). Under these conditions, the climate is too hot and dry to support the perennial grasses characteristic of steppes. Shrubs dominate on zonal soils in deserts, and if grasses are present, they are typically annuals rather than perennials (Daubenmire 1978).

Each of these three ecosystems, the midwestern steppes, and southwestern deserts, are characterized by a distinctive seasonal pattern. In figures 2, 3, and 4 mean monthly values for

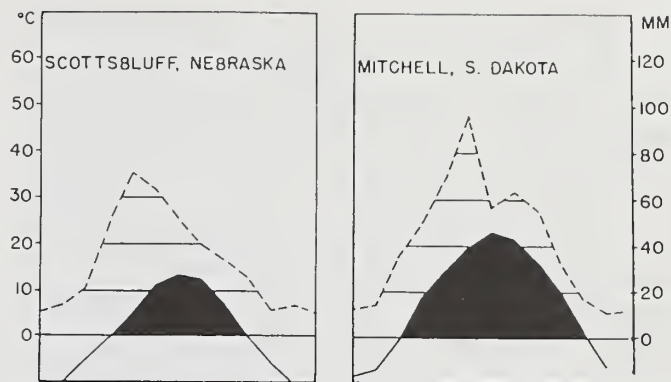


Figure 2. Seasonal trends of mean monthly temperature and precipitation at stations representing Midwestern steppe vegetation. Solid line= temperature; broken line= precipitation. From Daubenmire, *Plant Geography*, 1978.

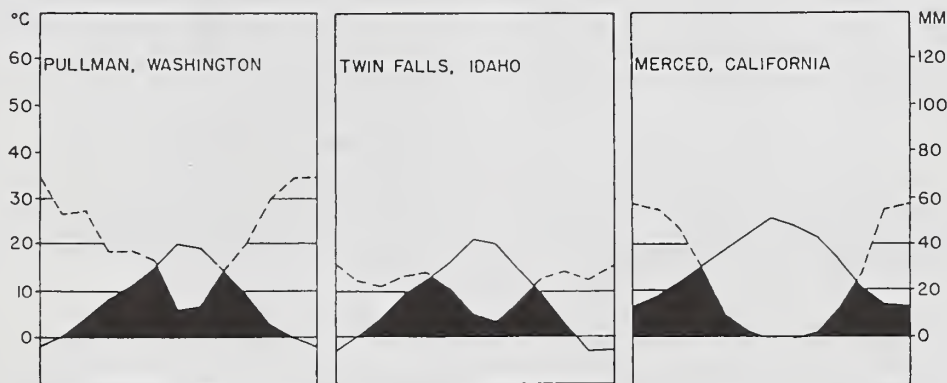


Figure 3. Seasonal trends of mean monthly temperature and precipitation at stations representing western steppe vegetation. Solid line= temperature; broken line= precipitation. From Daubenmire, *Plant Geography*, 1978.

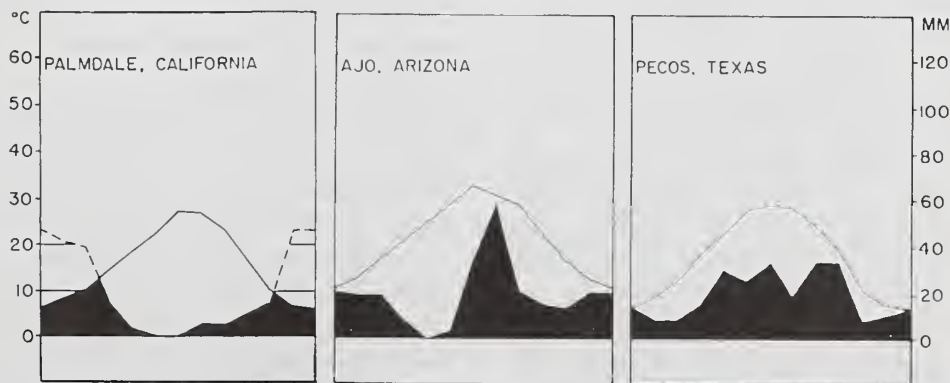


Figure 4. Seasonal trends of mean monthly temperature and precipitation at stations representing desert steppe vegetation. Solid line= temperature; broken line= precipitation. From Daubenmire, *Plant Geography*, 1978.

temperature (solid line) and precipitation (broken line) are plotted throughout a year. These diagrams provide information about both the amount and the timing of precipitation; unfortunately they do not reveal anything about year-to-year variability, which would be useful.

In the steppe ecosystems located east of the Rocky Mountains, precipitation peaks when temperature is high, that is, in spring or summer (fig. 2). The steppes located to the west of the Rockies, however, are characterized by summer drought; note that precipitation in this region is lowest in summer, when temperature is highest (fig. 3). This difference in the seasonal timing of precipitation has important consequences that are discussed below.

In the deserts of western North America, a rainy season may occur in autumn, winter, or summer (fig. 4); however, the amount of annual precipitation is highly variable. This variability has important consequences for desert organisms, which I will discuss shortly.

PRODUCTIVITY AND SENSITIVITY TO DISTURBANCE

Climate influences productivity both directly, through its influence on plant phenology, and indirectly, through its influence on soil development. Where primary productivity is low, as in deserts and some steppe communities, sensitivity to disturbances that remove vegetation and to invasion by exotic species that exploit resources unavailable to native organisms is high. For example, arid rangelands have been adversely impacted by introduced feral burros (*Equus asinus*), which are able to utilize high-fiber foods that cannot be digested by native ungulates (Seegmiller and Ohmart 1981). Similarly, the alien shrub tamarisk, or salt cedar (*Tamarix* spp.), which is able to reach water sources that are unavailable to native plants, has disrupted plant communities and hydrology in arid rangelands in many parts of the West. Unlike native species, salt cedar extends deep roots to the water table and uses prodigious amounts of water. As a result, salt cedar invasions have been accompanied by major changes in local hydrological cycles (Vitousek 1986; Horton 1977).

CONSEQUENCES OF CLIMATE PATTERNS

The timing of productivity is as important a consideration as the magnitude of that productivity. For example, seasonal trends in productivity influence grassland fire regimes, because fires are most likely to occur when there is abundant, dry fuel available.

In addition, the timing of productivity has other important consequences for western steppe and desert ecosystems, because of its influence on the prevalence of biotic disturbances such as grazing, trampling, wallowing, and digging. If animals are unable to inhabit an area because of inhospitable climate or because of insufficient seasonal productivity, they may be entirely absent from the area, they may be seasonally absent (because they migrate elsewhere), or they may be present but temporarily inactive (because they undergo diapause or torpor). To illustrate this, let us consider the distribution, abundance, and annual cycles of bison (*Bison bison*) and prairie dogs (*Cynomys* spp.) in steppe communities.

Summer Precipitation vs. Summer Drought in Steppe Environments

Distribution of Bison Herds

Although small, scattered bands of bison formerly inhabited this region, sizable herds of bison or other large, hooved grazers never persisted west of the Rocky Mountains (Guthrie 1970; Gustafson 1972; Schroedl 1973). Mack and Thompson (1982) suggest that summer drought was the primary factor excluding large herds of bison from the steppes of the Intermountain West. The greatest energy demand for bison occurs in early summer during lactation; however, intermountain grasses set seed and dry up by early summer. Thus, there is insufficient forage available when bison cows need it most. Consequently, the grasses of the Intermountain West were never confronted with large numbers of bison or other massive mammalian grazers and never adapted to large-scale grazing, wallowing, and trampling (Mack and Thompson 1982). A variant of this explanation was proposed by Van Vuren, who suggested that low bison numbers west of the Rocky Mountains

resulted from a combination of low forage production and low recolonization rates following local extinctions in discontinuous habitat (Van Vuren 1987).

As a result of this lack of significant selective pressure from large herbivores, the dominant species of native intermountain grasses never evolved adaptations that allowed them to rapidly revegetate large disturbed areas. This lack of coevolution between ungulates and intermountain grasses left native grasses vulnerable to invasion by exotics when agriculture and livestock grazing disturbed the region's vegetation on an unprecedented scale (Daubenmire 1970; Mack 1981). In contrast to the native grasses, however, cheatgrass (*Bromus tectorum*), Kentucky bluegrass (*Poa pratensis*), and other Eurasian grasses had co-evolved with large herbivores and were well adapted to germinate in disturbed areas (Hulbert 1955; Mack 1981; Mack and Thompson 1982; Mack and Pyke 1983, 1984; Mack 1986; Pyke and Novak 1994). The vulnerability of the intermountain steppes to disturbance from agriculture and grazing, and to invasion by exotic plants is rooted in the evolutionary histories of the native steppe grasses, which have been profoundly constrained by summer drought.

Distribution and Annual Cycles of Prairie Dogs

The seasonal timing of productivity has also influenced the distribution and activity cycles of a group of smaller herbivores characteristic of steppes, the prairie dogs. Figure 5 shows the geographic range of the black-tailed prairie dog (*Cynomys ludovicianus*), superimposed upon the map of steppe vegetation presented in figure 1. Notice that the range of the black-tailed prairie dog coincides with the steppes characterized by summer precipitation, that is, the region where photosynthetically active forage is available throughout the summer. In this connection, it is interesting to note that black-tailed prairie dogs are active throughout the year unlike ground-dwelling sciurids that inhabit the steppes of the Intermountain West, such as the Columbian ground squirrel (*Spermophilus columbianus*) and the white-tailed prairie dog (*Cynomys leucurus*), and avoid the summer drought that characterizes this region by

undergoing seasonal torpor. Although hibernation in prairie dogs, ground squirrels (*Spermophilus* spp.), and marmots (*Marmota* spp.), is often thought of as an adaptation to reduce energy requirements during cold weather, Bintz (1984) has argued that water stress during summer also promoted the evolution of seasonal torpor.

I suggest that the availability of succulent forage throughout the warm season, combined with this species' relatively good physiological mechanisms for water conservation, may have influenced the seasonal cycle of the black-tailed prairie dog by allowing individuals to maintain year-long activity. In contrast, the congeneric white-tailed prairie dog (*C. leucurus*), which occurs in intermountain steppes, is an obligate hibernator; this underscores the association between summer drought and seasonal torpor among prairie dogs.

Furthermore, black-tailed prairie dog coterries display a high degree of social integration (King 1955) and the ability of black-tailed prairie dogs to maintain year-long activity is thought to have influenced the evolution of social behavior in this species. Michener (1983) has shown that among ground-dwelling sciurids, cohesive social behavior occurs in species in which different age and sex classes are active above ground simultaneously. She suggests that temporal overlap between age classes is a necessary condition for the evolution of social tolerance and space sharing in this group. In some ground-dwelling sciurids, the annual activity period lasts only a few months and different age and sex classes are active at different times. Under these circumstances, opportunities for cohorts to interact are severely limited because they encounter each other infrequently, and cohesive social behavior is unlikely to evolve.

In black-tailed prairie dogs, however, year-long activity allows for a prolonged period of interaction between different age and sex classes, thereby setting the stage for the evolution of highly social behavior. In contrast, hibernating white-tailed prairie dogs exhibit a low degree of seasonal coincidence between age and sex classes and lack the highly cohesive social behavior seen in black-tailed prairie dogs. Among prairie dogs in western North America, the species that occurs in regions with summer drought is a hibernator, with low overlap in the activity periods of different age and sex classes, and relatively asocial behavior.

However, the species that inhabits regions with summer rains is active throughout the year, experiences a high degree of overlap in the activity periods of different cohorts, and is highly social.

Like bison, black-tailed prairie dogs have a significant impact on the vegetation and associated fauna of the midwestern steppes (Agnew et al. 1986). Because of their wide distribution and high densities, prairie dogs are capable of significantly

modifying soils, vegetation, and associated fauna through their feeding and burrowing activities. The absence of a pronounced summer drought in the Great Plains steppes appears to have influenced both the distribution and the annual cycle of black-tailed prairie dogs, allowing them to be active throughout the year and to form highly social, dense aggregations; thus, acting as a significant agent of biotic disturbance.

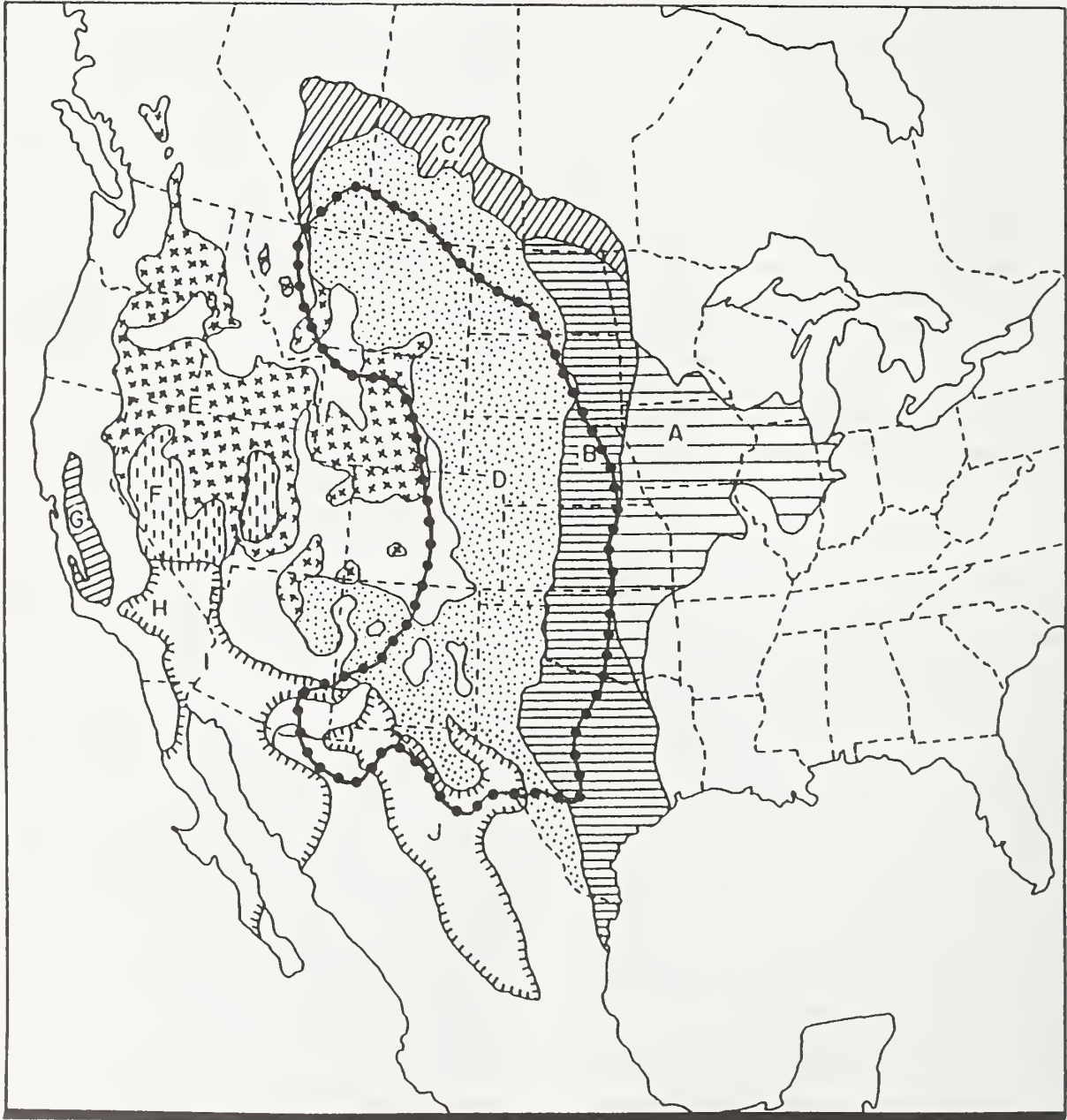


Figure 5. Distribution of the black-tailed prairie dog. B, C, D= Midwestern steppe; dotted line= outline of black-tailed prairie dog range.

VARIABLE PRECIPITATION IN DESERT ENVIRONMENTS

Life Cycles of Desert Plants

Because the amount and timing of precipitation in deserts are highly variable, strong selection pressure in this environment has favored adaptations that allow desert plants to take advantage of temporarily favorable conditions. These adaptations include the ability to endure long periods of unfavorable conditions as seeds or in a dormant vegetative state, and the ability to respond to appropriate environmental cues that signal the onset of favorable conditions by germinating or resuming growth (Louw and Seely 1982).

Timing of Reproduction in Desert Amphibians

Similarly, desert amphibians have evolved mechanisms that allow them to respond quickly to environmental cues signaling conditions favorable for reproduction. This characteristic makes them uniquely vulnerable to any disturbance that interferes with those environmental cues or causes them to be misinterpreted.

For example, desert amphibians often rely on acoustical cues, especially low-frequency sounds. Couch's spadefoot toad (*Scaphiopus couchi*) normally emerges from its burrows to breed in temporary ponds. This activity is cued by acoustical stimuli associated with thunderstorms. Off-road vehicles (ORVs) also produce low-frequency sounds and these travel long distances in desert air. Spadefoot toads exposed to motorcycle sounds respond by leaving their burrows; this could cause individuals that misinterpret ORV sounds to emerge at inappropriate times when temporary ponds are not available (Berry 1980). The reliance of this species on environmental cues that signal temporarily favorable conditions in a highly variable environment puts them at risk, resulting in an unusual vulnerability to novel disturbances that mimic those cues.

CONSEQUENCES OF CLIMATE CHANGE

Phenology and Persistence of Checkerspot Butterfly Populations

The examples presented above suggest that the ways in which an ecosystem's producers adapt to patterns of seasonality influence the distribution, abundance, and activity cycles of its consumers and that this coevolutionary history affects sensitivity to both biotic and abiotic disturbances. Because climate change has the potential to affect productivity and phenology, it has the potential to alter the frequency and intensity of disturbances. For example, it has been suggested that during the past two centuries increases in atmospheric CO₂ resulting from industrialization have contributed to increased cheatgrass productivity in intermountain steppe communities and a concomitant increase in fire frequency (Smith et al. 1987; Whisenant 1990; Mayeux et al. 1994).

It is difficult to retrospectively establish such connections between subtle changes in climate and changes in autecology and disturbance regimes. To clarify the effects of climate change it is necessary to switch to a finer scale of analysis. Studies of the Bay checkerspot butterfly (*Euphydryas editha bayensis*) in a western grassland ecosystem illustrate the mechanisms by which changes in phenology due to variation in climate determine population persistence for herbivores that are closely tied to the life cycles of their host plants.

These relationships between climate, plant phenology, herbivory, and population persistence have been demonstrated by Murphy and Weiss (1992). They draw on decades of data on the dynamics and ecology of Bay checkerspot populations to identify the mechanisms by which fluctuations in climate lead to local extinctions of Bay checkerspots.

The Bay checkerspot is restricted to patches of native grassland occurring on serpentine soils in California. For populations of this herbivore to persist, the development of larvae and host plants during California's moist, cool-weather growing season (figs. 1G and 3) must proceed synchronously. Eggs hatch in spring and larval growth and development depend upon the availability of succulent vegetation. Larvae must reach

influencing the distribution and availability of larval host plants.

CONCLUSIONS: CLIMATE AND SUSTAINABILITY

What does all this have to do with sustainable use of grassland ecosystems? First, the grassland ecosystems of western North America are climatically diverse with differences in productivity, seasonality, and disturbance regimes. If we are to use grasslands sustainably, we must understand the climatic and evolutionary constraints operating in each ecosystem and the resulting differences in resilience. Sustainable use cannot exceed productivity, which is constrained by climate. Furthermore, organisms are adapted to the disturbance regimes typical of the regions where they evolved.

The consequences of failing to understand that are illustrated in the Intermountain West. In this region novel land uses led to irreversible changes because of a dramatic alteration in disturbance

regimes. This occurred because of the introduction of livestock grazing and agriculture followed by invasions of exotic plants that had superior adaptations to the new disturbance regime. Disturbances created by resource use are likely to be sustainable if they imitate natural disturbance regimes in size, frequency, and intensity. Finally, rapid climate change has the potential to increase extinction rates for organisms adapted to current conditions that are unable to migrate elsewhere because of habitat fragmentation or poor powers of dispersal. In addition, rapid climate change has the potential to alter disturbance regimes.

ACKNOWLEDGMENTS

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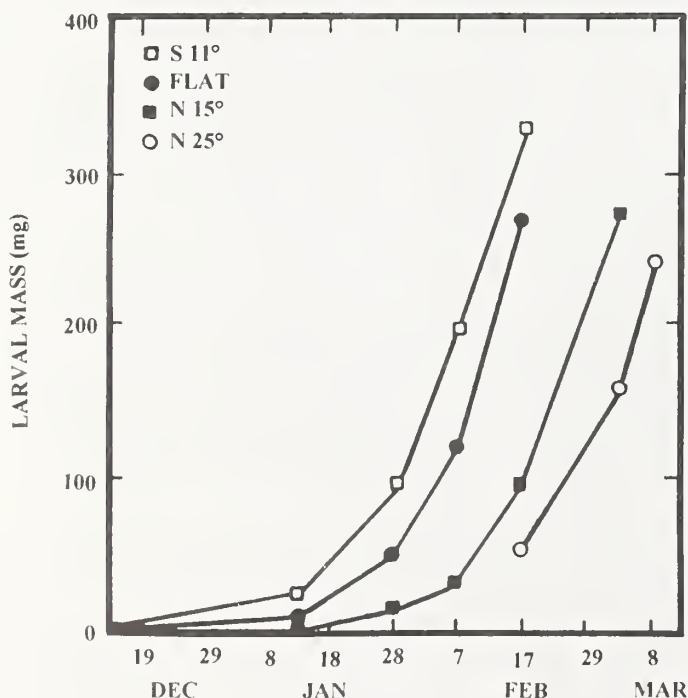


Figure 6. Growth of Bay checkerspot larvae on four slope exposures at Morgan Hill, 1987-88. From Murphy and Weiss. In: Peters and Lovejoy, *Global Warming and Biological Diversity*, 1992.

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Grazing effects on grassland ecosystems

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Abstract.—In this study, we used a modified version of a meta-analysis (compilation and analysis of the literature in which an individual area is subjected to the disturbance and its response is noted) to analyze grazing effects on grassland ecosystems. Prior efforts have focused on one aspect of ecosystem behavior such as productivity or species diversity. In this analysis, we examined several components of ecosystem function that are seldom explored including measures of nutrient cycling and soil compaction. In general, cattle grazing appears to decrease production measures, increase soil compaction, and have mixed impacts on nutrient cycling rates. In studies that examined nutrients, cattle grazing tended to increase amounts of available phosphorus and nitrogen while decreasing the amounts of other nutrients. We located several studies of sheep grazing and found that their impacts are not much different from those of cattle.

INTRODUCTION

To understand ecosystem function with respect to abiotic and biotic disturbances, two different methodologies have been followed. First, an empirical method has been used in which an individual area is subjected to the disturbance and its response is noted. A more recent technique (a meta-analysis) involves compilation and analysis of the literature in which the former type of study was done (Fernandez-Duque and Voleggia 1994). In this study, we used a modified version of this second procedure to analyze grazing effects on grassland ecosystems.

Prior efforts have focused on one aspect of ecosystem behavior such as productivity (Lacey and Van Poollen 1981; Coughenour 1991; Painter and Belsky 1993) or species diversity (Milchunas and Lauenroth 1993; Fleischner 1994). In this analysis, we examined several components of ecosystem function that are seldom explored including measures of nutrient cycling and soil compaction.

It is critical that many components be examined because they may provide insight into ecosystem health trends sooner than can be determined by looking at only one type of ecosystem function. For example, species diversity is often a poor indicator of ecosystem response to grazing because by the time there is any observable effect on species diversity, significant ecosystem damage may have occurred (Milchunas and Lauenroth 1993). One way to examine this is to consider the classical species response curves in relation to a resource. In these Gaussian curves, as resource quantity is reduced below optimum, the abundance of a species decreases, as seen in figure 17.1B of McNaughton (1993). But, as occurs with these types of responses, resource quantity can decrease dramatically before the species disappears from the system; even if that species has a narrow resource response curve. The processes associated with a resource (e.g., PAR, nutrients, etc.) would also be affected. Thus, species loss is preceded by the changed processes, rather than causing the changed processes.

There are, however, numerous examples that point to change in ecosystem processes due to species loss (Martinez 1995). For example, food

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web structure may depend upon one or more species, without which system structure and function collapse. Examining changes in species diversity as a result of changes in ecosystem processes does not negate the alternative view. Both opinions must be examined to understand the effects of disturbance on ecosystems (Jones and Lawton 1995). From this dual perspective, we can examine the ecosystem-level impacts of herbivory.

METHODS

We examined recent papers for discussion of the response of multiple ecosystem processes to grazing. Grazing included that by ungulates (primarily domesticated), insects and birds, or large-scale clipping or mowing experiments. A large number of journals were searched including *Journal of Range Management*, *Ecology*, *Journal of Wildlife Management*, *BioScience*, *Journal of Ecology*, *Journal of Applied Ecology*, *Functional Ecology*, *Oecologia*, *Oikos* and *Ecological Applications*. Journals were chosen based upon the likelihood that they would report large-scale studies. We did not include single-species response papers, instead we focused on recent papers to avoid reanalyzing those that may have been included in other summary analyses.

Each paper was examined for evidence of the following parameters: stocking rate (as defined by Heitschmidt and Taylor 1991), evidence of soil compaction, nutrient cycling, primary and secondary production, and effects on community structure. The grazing system (Heitschmidt and Stuth 1991) and location of the study were also noted. Standard meta-analysis procedures (Fernandez-Duque and Valeggia 1994) could not be used since the data in each of the categories varied. For example, data on grazing impacts on nutrient cycling varied from narrative evaluations (more digestible forage) to the size of soil pools of a nutrient. Therefore, what we present here is a narrative review of trends among these different factors.

The nomenclature we use is common in domestic grazing management. The abundance of animals is stocking density; grazing pressure is the numbers of animals per unit plant production; stocking rate is the number of animals per unit

land area per unit time (Coughenour 1991). A grazing system includes defined periods of grazing or deferment in one or more pastures (Heitschmidt and Stuth 1991).

RESULTS

Seventeen studies are described in table 1. These, along with the 16 reviews described previously (Wallace and Dyer 1995), indicate that few studies examined multiple parameters. In general, cattle grazing appears to decrease production measures, increase soil compaction, and have mixed impacts on nutrient cycling rates. In studies that examined nutrients, cattle grazing tended to increase amounts of available phosphorus and nitrogen while decreasing the amounts of other nutrients. Other large herbivores were not studied to the same extent as cattle. We located several studies of sheep grazing and found that their impacts are not much different from those of cattle. Interestingly, stocking rates of sheep tend to be higher than those of cattle.

Few studies have examined the impact of wildlife grazing or insect herbivory on ecosystems. In one study, insects increased nutrient cycling rates more than ungulate herbivores (Brown 1994).

Out of the 34 studies we examined (Wallace and Dyer 1995), only 12 observed more than one parameter response to herbivory. Approximately half of these examined plant production and species composition, but did not examine nutrient levels, soil compaction, or below-ground biomass. Useful longevity indicators, such as root biomass and soil C, decreased in studies by Dormaar et al. (1994) and Mitchell et al. (1994). However, other soil nutrients, particularly measures of soil N, increased in response to grazing (Mitchell et al. 1994; Dormaar et al. 1994; Brown 1994; Wallace and Dyer 1995). Available phosphorus and calcium were increased by grazing in one study (Westenskow et al. 1994).

DISCUSSION

Herbivory impact on ecosystems is a controversial topic with long-lived debates focusing on issues such as plant compensation for herbivory

Table 1. Impacts of grazing systems on ecosystem level parameters. If the herbivore species is not named explicitly, then cattle were grazed. Cattle were grazed with other species in those systems marked as various herbivore species. Where responses are preceded by a sign (+ or -), the response is the process seen in a grazed area relative to an ungrazed area. Where no sign is present, the response is the absolute value measured in the treatment.

Name/Date	System	Location	Stocking rate	Soil compaction	Nutrient cycling	Production Plant	Animal	Community structure
Wallace & Dyer 1995	Various	Various	Various	Increased	Generally decreased	Less	More	Reduction in grass cover
Fleischner 1994	Various	Various	Various					Reduction in overall diversity
Anderson & Radford 1994	Continuous	England	Various			-28.8% Cover		
Mitchell et al. 1994	Continuous ducks	Texas	Heavy Light		Increase soil N	Rhizome biomass -23.7% -5.1%		Increase in species richness
Brown 1994	Insect herbivory	Minnesota			+8.9% soil N +56.5% soil NO ₃ +18.7% plant N uptake			Increase in species richness
Lacey & Van Poollen 1981	Various	Various	Moderate			-68%		
Brown & Stuth 1993	Continuous	Texas	.217 AU/ha .435 AU/ha .571 AU/ha			No overall reduction		
Dyer & Wallace (In review)	Various	Various	Various			+47% Monocots +17% Dicots		
Bullock et al. 1994	Put & take sheep	England	Heavy Light			Increase in dicot abundance		
Pickup 1994	Continuous	Australia	660 cattle/ 170 km ²			-11.6% Forage Index ¹		
Vickery et al. 1994	Continuous	England	186.7 LUD/ha cattle 262.8 LUD/ha sheep		Protein 15.4% 14.8%	g/m ² 68.5 51.7		
Smith & Rushton 1994	Rest/rotation	England	100 ewes/ 16.2 ha sheep			Biomass -34.7%		Increased species richness
Pfeiffer & Steuter 1994	Continuous bison	Nebraska	1 AUM/ha/yr			Biomass (unburned) -15.1% grass +1.6% forb		

Table 1. Cont'd.

Name/Date	System	Location	Stocking rate	Soil compaction	Nutrient cycling	Production Plant	Animal	Community structure
Volesky et al. 1994	Frontal continous rotational	Oklahoma	6.7 head/ha			kg/ha 1390 1400 1510	kg/ha/day 281 6 321	
Westenskow et al. 1994	Continous elk	Oregon			+51% Ca,P	kg/ha -37.8%		
Austin et al. 1994	Continous delayed (horse) deer deer & horse	Utah	5.3 horses/ 0.1 ha			-50.0% +165.4% +5.3% +178.4%		
Dormaar et al. 1994	Continous	Alberta	Moderate	-5.5%	-14.4% C -15.5% N -16.4% NO ₃ +30.9% NH ₄ +22.5% P	-16.4% Roots		Increase in species richness
Papolizio et al. 1994	Continous	Colorado	621 AUM					-9.3% species number

¹ Forage Index for Pickup (1994) describes the relative attractiveness of each species for grazing multiplied by its abundance and summing over all species for a site.

(Belsky 1986; McNaughton 1986; Dyer et al. 1993) and livestock herbivory on public lands (Gillis 1991; Wilcove 1994). We do not propose to reopen these arguments, but instead to examine how to answer questions associated with them. Since many of the proponents and opponents of livestock grazing profess a strong desire to protect the ecosystem (still loosely defined in ecological circles [Allen and Hoekstra 1992]), it is incumbent upon scientists focusing on this topic to provide policy makers with information concerning grazing impacts on ecosystem processes.

PRODUCTIVITY

Many of these processes have different temporal scales. Productivity is strongly controlled by climate and greatly influences the rate of herbivory (McNaughton et al. 1990; Cebrián and Duarte 1994). Productivity also has a strong seasonal component and can be analyzed on a shorter daily

time-step. However, given the variance in productivity among these different time scales, it may be a poor predictor of the longevity of grazing management protocols. Production and other ecosystem parameters have been noted to pulse in other systems (Odum et al. 1995) and should be expected to do so in grazing systems.

COMMUNITY STRUCTURE AND BIODIVERSITY

Many authors have also examined plant community structure under the supposition that species will integrate a number of other processes and can indicate long-term ecosystem health (Tracy and Brussard 1994; Brown 1995). However, this view has been strongly questioned. Milchunas and Lauenroth (1993) examined over 300 grazing studies that analyzed plant community responses and found that species composition showed few strong correlations with critical ecosystem param-

eters such as net primary production, consumption, or evolutionary grazing history. In a strongly worded statement they proposed that, "Current management of much of the world's grazing lands based on species composition criteria may lead to erroneous conclusions concerning the long-term ability of a system to sustain productivity."

Scarnecchia (1994) also stated that we would have greater power in analyzing grazing systems using a combination of variables rather than relying on single-variable analyses.

COLLECTION AND USE OF COMPLEX DATA SETS

How do we interpret multiple variable studies? Do we give one variable more weight than another? This is one of the critical issues in linking species-and ecosystem-level processes (Jones and Lawton 1995). Several key elements are missing that are necessary to accomplish an overall interpretation in the data set we have accumulated.

First, some uniformity of methodology and units is needed. Meta-analysis procedures are a powerful technique to draw conclusions from large, disparate data sets. However, this power is diminished if the variables analyzed do not have an associated variance (Fernandez-Duque and Valeggia 1994). Therefore, narrative evaluations should be avoided and quantification of parameters should be done using similar methods among studies. For example, sometimes plant productivity estimates include estimates of the amount of material removed, but more often they do not. True estimates of primary production in grazed environments require some quantification of removal rates.

Second, many variables that provide an estimate of longevity of the grazing system are difficult to measure and are therefore usually not measured. We found only two studies in our data set that explicitly addressed root biomass (Dormaar et al. 1994; Mitchell et al. 1994). Root and soil carbon are long-term, slowly-cycling parameters that can indicate trends in system aggradation or degradation. Few if any studies examined below-ground herbivory despite early requests in the literature for such data collection (Dyer 1979). In addition, few studies explicitly examined the rates of sec-

ondary productivity in systems (McNaughton et al. 1990), although this is critical to examining energy flow patterns. For example, invertebrates are more efficient at converting plant biomass to herbivore biomass than are vertebrate grazers (McNaughton et al. 1990; Brown 1994), which leads to a more efficient flow of energy, nutrients, and information. This may be a scale-related phenomenon in which small-scale herbivores with short life spans have a greater impact on the nutrient regime of grazed systems than herbivores that operate at larger scales and have longer life spans. This spatial scale would most certainly be expected to interact with a temporal scale, particularly in pulsed systems (Odum et al. 1995).

Finally, the grazing systems used in each study must be explicitly described. This includes a uniform quantification of grazing intensity with appropriate use of control plots and careful monitoring of herbivory timing. With this level of quantification, some of the objections of those concerned about grazing (e.g., Painter and Belsky 1993; Wilcove 1994) can be addressed.

Our data set illustrates many of the problems described above and gives mixed results in terms of how herbivores affect ecosystems. In many systems, plant production measures are lower in grazed areas than in ungrazed (table 1). Given the caveats listed above, until we understand where each of these systems is in the two-dimensional space relating productivity to herbivory (Risser 1993), interpretations concerning the effects of grazing as a whole are impossible. Increases in species richness were noted for several systems; decreases were noted in others. In some systems, greater richness was attributed to the increase in numbers of unpalatable forbs and to the increase in bare ground on which they could germinate (Anderson and Radford 1994; Bullock et al., 1994). However, exactly the opposite was found in other systems (Austin et al., 1994; Smith and Rushton 1994).

Given the inconsistencies in the approaches to collecting and analyzing data, we feel that we can not develop global conclusions from the information compiled. However, it is critical to note that grazing intensity in each system must be matched to the capability of the system to sustain that use level. We hope that the problems illustrated in this exercise will encourage others to collect data

needed by managers to make decisions about the sustainability of their own system. Additionally, we hope that managers realize that what is sustainable in one system, will not necessarily be so in others. We are concerned that given the negative response of the longevity measures of soil C, etc., some of the systems we have examined appear to be grazed at levels that may be unsustainable over the long-term. This adds a strong sense of urgency to our endeavors.

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Ecology of fire in shortgrass prairie of the southern Great Plains

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Abstract.—The ecology of fire in shortgrass prairie of the southern Great Plains includes a complex interaction between the shortgrass prairie ecosystem and its inhabitants, all inextricably linked to land-use patterns. The history of the relationship between man and fire has been filled with ambivalence and mistrust, along with an appreciation of the power of fire as a management tool. Fire is now used as a management tool on at least a limited scale in all areas of North America, and perhaps nowhere is the role of fire in community organization more widely acknowledged than in grassland ecosystems. Numerous studies have indicated that plant, arthropod, bird, and mammal populations and communities respond differentially to disturbance by fire, due in part to the fact that fire can have both direct and indirect effects. Therefore, grassland fires may directly or indirectly elicit major or minor changes in population or community structure depending upon the vagility, life history and trophic level of the organisms, degree of modification of habitat, and the timing, extent, and frequency of the fire. Interpretation and application of the results of previous studies of fire effects are constrained by the descriptive nature of these studies. Field-based experimental research is needed to help resource managers predict community responses to fire.

INTRODUCTION

"The effect of fire must be regarded as having been always operative in the Great Plains region. Fires are started by lightning during almost every thunderstorm, and the advent of man, has, if anything, tended to check rather than to increase their ravages."

(Shantz 1911)

"Fire is rightly comparable to a two-edged sword. While it may be used to good advantage at times to obtain definite desired results, its abuse, or careless uncontrolled use, may be productive of great harm."

(Stoddard 1931)

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The history of the relationship between man and fire has been filled with ambivalence and mistrust, along with an appreciation of the power of fire as a management tool. Native Americans frequently started grassland fires to modify habitat and to aid in hunting activities by both driving and attracting wild game (Bahre 1985; Pyne 1982). Early non-native attitudes regarding fire were colored by the European philosophy of fire suppression as being tantamount to fire management. In the past 50 years attitudes have changed significantly regarding the use of fire. Fire as a management tool was reintroduced into North America first in the southeastern U.S. (1930s), following research by scientists, including Chapman (1926, 1932, 1936), the first scientist to provide a scientific basis for prescribed burning. Further support for burning in the 1930s was provided by the works of Green (1931), Heyward (1936, 1937, 1939) and Stoddard

(1931), who published on the effects of fire on forest structure, soil, and wildlife, respectively (Wright and Bailey 1982). Yet, from 1940 to the early 1960s there were still many followers of the European philosophy who feared fire would be misused (Wright and Bailey 1982).

Biologists began taking a more benign view of fire in North America starting in the early 1960s with the release of the Leopold Report. The report enlightened the general public about negative effects of total fire suppression in plant communities, including excessive fuel loading, declining wildlife species diversity, and encroachment of shrubs and trees into grasslands. Fire is now used as a management tool on at least a limited scale in all areas of North America (Leopold et al. 1963; Wright and Bailey 1982). And perhaps nowhere is the role of fire in community organization and development more widely acknowledged than in grassland ecosystems (McPherson 1995).

The origin of the North American grasslands can be traced to the Miocene-Pliocene transition, perhaps 7-5 million years before present (YBP), associated with the beginning of a drying trend. The increased aridity resulted from the chilling of the ocean as the Antarctic ice sheet spread and from the Miocene uplift of the Rocky Mountains, which served as a partial barrier to moist Pacific air masses. Grasses are generally better adapted to drought than most tree species, and the spread of the grasslands occurred at the expense of forest vegetation (Axelrod 1985; Anderson 1990). Fire interacts with other factors including topography, soil, insects, herbivores (rodents, lagomorphs), and herbaceous plants to restrict woody plant establishment in grasslands (Grover and Musick 1990; McPherson 1995; Wright and Bailey 1982). Currently, there is general agreement that fire is necessary (though usually not sufficient) to control the abundance of woody plants and maintain most grasslands. In the absence of periodic fires, grasslands usually give way to dominance by woody plants (McPherson 1995). However, the question of how fire affects rangelands still needs to be fully addressed (McPherson 1995; Steuter and McPherson 1995). This literature review is intended to discuss the possible role of fire in structuring plant and animal communities in shortgrass prairie of the southern Great Plains.

HISTORY

Reliable historical records of fire frequencies in prairie of the southern Great Plains are not available because there are no trees to carry fire scars from which to estimate fire frequency. However, the recent fire history of the northern Great Plains was reconstructed by examining charcoal fragments taken from lake sediment cores (Umbanhowar 1996). The same method could be used in lakes and playas to reconstruct the fire history of the southern Great Plains. Results of Umbanhowar's research indicated that post-settlement patterns of charcoal deposition were highly variable but generally much lower than pre-settlement intervals, suggesting settlement resulted in a decrease in the number of fires due to active fire suppression. This conclusion is similar to that of Bahre (1991), who with the use of historical accounts, concluded fire size and frequency have diminished greatly in desert grasslands since the 1880s. Removal of available fuel by livestock overgrazing most likely also contributed to the post-settlement decline in fire frequency.

Historical accounts of fires by early settlers in the southern Great Plains do exist. However, such accounts are often anecdotal and biased toward documenting particularly large or destructive fires (McPherson 1995; Wright and Bailey 1982). Historical records of disturbance by fire may not be crucial for present-day land management concerns. Disturbances that caused past vegetation change (e.g., heavy cattle grazing, decreased fire frequency, specific timing of precipitation) may fail to produce similar responses today, because of profound changes in physical and biological environments over the last century. These changes include increased concentrations of atmospheric greenhouse gases (i.e., CO₂, methane), increased abundance of native (i.e., woody perennial), and non-native plants (i.e., lovegrasses, buffelgrass, *Cenchrus ciliaris* several herbaceous dicots), and decreased abundance of some plant and animal species (McPherson (in press); Weltzin and McPherson 1995). Furthermore, changes in economic, social, and political conditions have also had an impact on land use practices.

Consider the many factors influencing the extreme vegetation change in the Great Plains 100 years ago. The large migration of settlers into the

Plains and the expansion of cultivated and heavily grazed areas occurred during comparatively wet periods following the end of the Civil war in 1865 (Rasmussen 1975; Washington D.C. 1936). From 1864 through 1891, El Niño³ activity was unusually strong and frequent (Quinn et al. 1987) producing wetter than average spring and fall seasons in the Southwest. The succession of wet years and good harvests may have acted to accelerate settlement, when farmers and ranchers mistook a prolonged El Nino event for the permanent climate. In 1934 and again in 1936 drought conditions in the Great Plains area of the United States, including the southern Great Plains, became so severe that it was necessary for the Federal Government to take emergency intervention (Rasmussen 1975). To this effect, the government created the Great Plains Drought Area Committee in the 1936. The following is an excerpt from *The Future of the Great Plains* (Washington, 1936). This report from the U.S. Great Plains Committee, analyzed the factors causing the severe "dust bowl" changes in vegetation in the Great Plains:

The present situation in the Great Plains area is the result of human modification of natural conditions. Prior to the coming of the white man, and to a large extent prior to about 1866, man did not greatly alter conditions on the Plains. The Indians did two things: they killed buffalo and they sometimes set fire to the grass. They do not seem to have reduced the number of buffalo seriously, and though their fires may have influenced the nature of the vegetation they did not destroy primitive grass cover. There is no evidence that in historic times there was ever a severe enough drought to destroy the grass roots and cause wind erosion comparable with that which took place in 1934 and 1936; that phenomenon is chargeable to the plowing and over cropping of comparatively recent years.

³ El Niño-Southern Oscillation (ENSO) events are global-scale climatic anomalies that recur at intervals of 2 to 10 years and at varying intensities (Philander 1983), with weak tradewinds and high sea-surface temperatures off the western coast of the Americas. Southern Oscillation is measured as the normalized differences in monthly mean pressure anomalies between Tahiti, French Polynesia and Darwin, Australia. El Niño and Southern Oscillation are linked in a global climate complex of changing ocean currents, ocean temperatures, atmospheric pressure and temperature gradients. Climatic effects of ENSO are highly variable, sometimes leading to droughts in some regions and flooding in others (Swetnam 1990). In the southwestern United States, ENSO events are most consistently related to wetter than average spring and fall seasons (Andrade and Sellers 1988).

The report goes on to state that the Great Plains are estimated to have been nearly 100 percent overstocked with cattle in 1935. And with the advent of tractors, combines, and other powerful machinery, farmers were able to plant and harvest a much larger acreage than before. Therefore, soil not previously plowed was exposed to the wind with no cover crop to protect it between seasons. The effects of wind erosion were more disastrous in the southern Great Plains than further north, but the exposed and friable soils almost everywhere were washed or blown to some extent. Many itinerant farmers put in crops, but because of low prices, did not return to harvest what they had sown, leaving the soil partially exposed to the drying and eroding winds.

The report further stated that there were approximately 24,000 crop farms, covering a total of 15 million acres (37,065,000 ha), which should no longer be plowed. It recommended that the Federal Government continue the policy of purchasing scattered crop farms and other appropriate lands in areas devoted largely to grazing, the formation of cooperative grazing associations, and the creation of erosion control districts (Rasmussen 1975).

Other federal programs designed in part to protect the environment, and that directly affected the Great Plains, include: the Bankhead-Jones Farm Tenant Act of 1937, that included a directive to retire submarginal land, and under which most national grasslands administered by the United States Forest Service were acquired; The Taylor Grazing Act of 1934, which gave the Department of the Interior authority to regulate grazing on the public domain to stop injury to public grazing lands by preventing overgrazing and soil deterioration; and establishment of the Soil Conservation Service in 1935 which was to provide technical range management assistance to private landowners.

Southern Great Plains: Shortgrass Prairie

Natural History

The southern Great Plains includes the eastern third of New Mexico, the northern two-thirds of Texas, and most of Oklahoma. The region can be divided into shortgrass, mixed, and tallgrass prairie categories (fig. 1). Within the area, the shortgrass prairie lies west of the 100 meridian

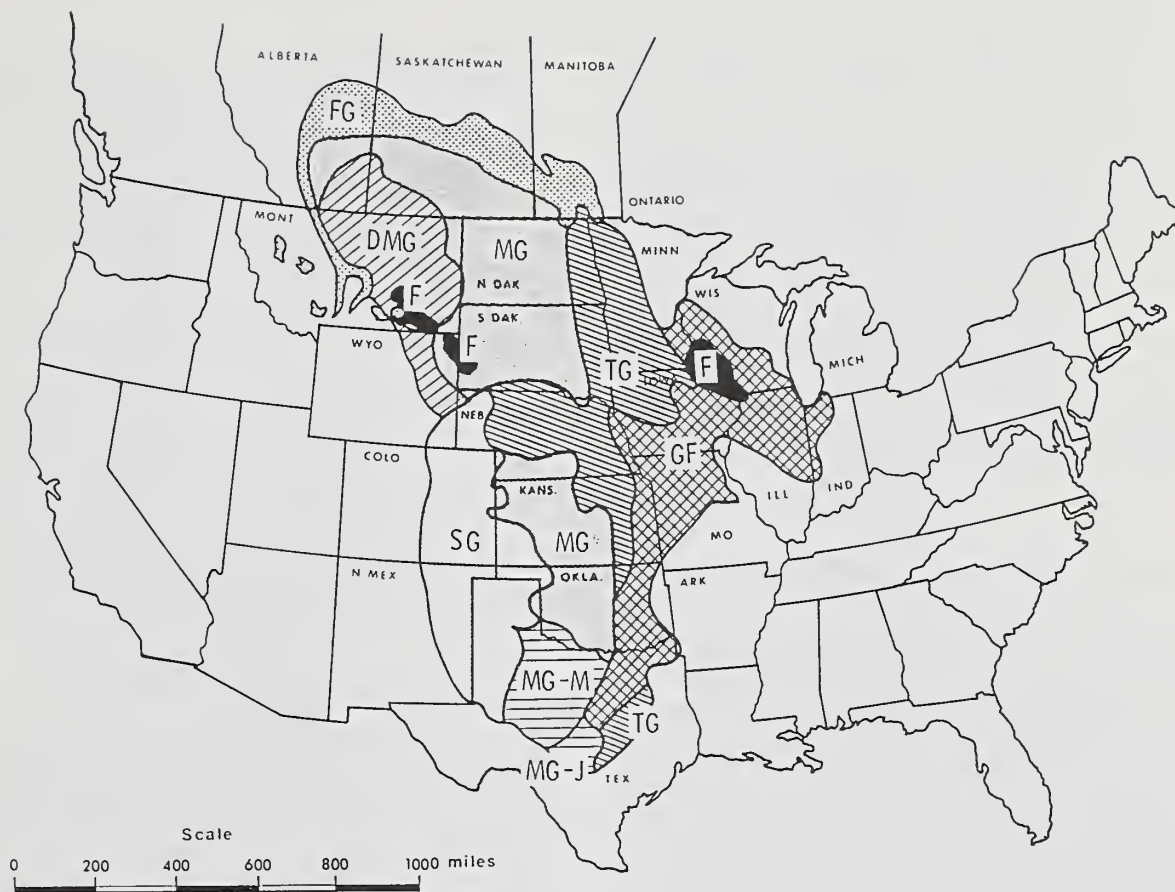


Figure 1. Natural vegetation of Great Plains grasslands (Wright and Bailey 1980). Modified from Kuchler (1965) and Rowe (1972). DMG, Dry mixed grassland; F, Forest; FG, Fescue grassland; GF, Grassland forest; MG, Mixed grassland; MG-J, Mixed grassland-juniper-oak; MG-M, Mixed grassland-mesquite; SG, Short grassland; TG, Tall grassland.

(Wright and Bailey 1982). It is estimated that less than 23% of true shortgrass prairie still exists in native vegetation (NGMR 1995). The grassland is semi-arid; annual precipitation in shortgrass prairie ranges between 15 and 20 inches (38 to 51 cm). Except for sandy soils in southeastern New Mexico and the Canadian River country in northern Texas and western Oklahoma, soils are primarily clay loams, silt loams, and sandy loams. A caliche layer is frequently present at 20 to 36 inches (51 to 91 cm) in the fine-textured soils. Most of the area is tableland that is 4,000 to 6,000 ft (1,200 to 1,829 m) in elevation (south to north) on the western edge, and slopes eastward to 3,000 ft (915 m) on the edge of Llano Estacado in Texas. Dominant grasses are buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*), with varying

amounts of threeawns (*Aristida* spp.), lovegrass (*Eragrostis* spp.), tridens (*Tridens* spp.), sand dropseed (*Sporobolus cryptandrus*), sideoats grama (*Bouteloua curtipendula*), tobosagrass (*Hilaria mutica*), galleta (*H. jamesii*), vine-mesquite (*Panicum obtusum*), bush muhly (*Muhlenbergia porteri*), and Arizona cottontop, *Digitaria californica* (Bailey 1995; Wright and Bailey 1982).

Forbs can be abundant during wet years, but they are seldom a major component of the short-grass prairie. Common forbs include annual broomweed (*Xanthocephalum dracunculoides*), false mesquite (*Hoffmanseggia densiflora*), western ragweed (*Ambrosia psilostachya*), horsetail conyza (*Conyza canadensis*), warty euphorbia (*Euphorbia spathulata*), silver-leaf night shade (*Solanum elaeagnifolium*), manystem evax (*Evax multicaulis*),

woolly plantago (*Plantago purshii*), dozedaisy (*Aphanostephus* spp.), goosefoot (*Chenopodium* spp.), croton (*Croton* spp.), summercypress (*Kochia scoparia*), and globemallow (*Sphaeralcea* spp.) (Wright and Bailey 1982).

Dominant woody plants are honey mesquite, sand shinnery oak (*Quercus havardii*), sand sagebrush (*Artemisia filifolia*), perennial broomweed (*Gutierrezia sarothrae*), yucca (*Yucca* spp.), and fourwing saltbush (*Atriplex canescens*). Cactus (*Opuntia* spp.) can also be abundant. The prevalent species include pricklypear (*Opuntia polyacantha*), brownspine pricklypear (*O. phaeacantha*), walking-stick cholla (*O. imbricata*), and tasajillo (*O. leptocaulis*) (Wright and Bailey 1982).

VEGETATION RESPONSES TO FIRE

All previous research on vegetation responses to fire in shortgrass prairie of the southern Great Plains is based on single-fire or burned vs. unburned (i.e., non-experimental) research. Most of this research was conducted before 1980, and was primarily interested in the use of fire as a tool to increase forage value of vegetation. Results of these studies are hampered by weak inference (Platt 1964), and therefore must be interpreted cautiously. A more reliable approach would be to use experiments designed specifically to test hypotheses about vegetation responses to fire.

One such example of this type of research is a study in progress by Brockway (1995) on the effects of restoring fire to shortgrass prairie on the Kiowa National Grasslands in northeastern New Mexico. The study employs a completely randomized experimental design, with seven treatments and five replicates, to analyze how grassland nutrient cycling, plant productivity, and community structure are affected by fire frequency and season of burn. Research on the effects of fire on tallgrass prairie and desert grassland by Long-Term Ecological Research Programs at the Konza Prairie Research Natural Area in Kansas, and the Sevilleta National Wildlife Refuge in New Mexico, respectively, also use the experimental method to answer questions concerning vegetation response to fire. More of these types of studies are needed in the southern Great Plains to develop an accurate picture of how fire affects the shortgrass prairie ecosystem.

EARLY RESEARCH

Considerable research was conducted to address fire effects in shortgrass prairie before 1980. In general, these studies indicate that fire leads to decreased herbaceous production for 1-3 years, and herbaceous response is influenced strongly by precipitation. Fires also contribute to reductions in woody plant cover and increases in density and diversity of herbaceous dicots.

Following a spring wildfire in shortgrass prairie, when the soil was dry, Launchbaugh (1964) concluded that fire caused short-term declines in plant biomass. It took three growing seasons for a burned buffalograss-blue grama community to return to a level comparable to that of unburned areas. Similar results of burning in prairie were reported in west-central Kansas (Hopkins et al. 1948). Following a wildfire in New Mexico when the moisture balance was more favorable, Dwyer and Pieper (1967) found that biomass production of blue grama was reduced only by 30 percent during the first year growing season following the burn. Blue grama biomass returned to pre-burn status with above-average precipitation the second year after burning.

Results from prescribed burns in Texas during years with above-normal winter and spring precipitation showed that buffalograss and blue grama tolerated fire with no loss in herbage yield at the end of the first growing season (Trlica and Schuster 1969; Heirman and Wright 1973; Wright 1974; Wright and Bailey 1980). The tolerance of most grass species to fire in the shortgrass prairie, under different moisture regimes, appears to be similar to that of buffalograss and blue grama (Wright and Bailey 1982).

In the southern Great Plains, patches of sandy soil are common among the heavy clay soils that are dominated by buffalograss and blue grama. The sandy soils are dominated by sand bluestem (*Andropogon hallii*), little bluestem (*A. scoparius*), switch grass (*Panicum virgatum*), and sand shinnery oak. Burning generally increased production of sand bluestem and switchgrass about 300 lb/acre (337 kg/ha) and, decreased production of little bluestem, with a net increase in total forage of 20 percent (McIlvain and Armstrong 1968; Wright and Bailey 1982).

ANIMAL RESPONSE TO FIRE

Arthropods, birds, and mammals all play important roles in ecosystem functioning of shortgrass prairie, serving as decomposers, pollinators, herbivores, predators or prey. They cycle nutrients and form valuable links among trophic levels.

Numerous studies have indicated animal species, populations and communities respond differentially to disturbance by fire, due in part to the fact that fire can have both direct and indirect effects. Direct effects are acute but ephemeral i.e., fire induced mortality. Indirect effects (i.e., alterations in habitat) are long-lasting and usually more important. Therefore, grassland fires may directly or indirectly elicit major or minor population or community structure changes depending upon the vagility, life history and trophic level of the animal, and the timing, extent and intensity of the fire.

Arthropods

Little is known about the diversity of arthropods on southwestern rangelands. Available data indicate that species diversity for most groups of rangeland arthropods is higher in the Southwest than in other parts of the country (Parmenter et al. 1994). Our surveys have already yielded close to 100 species of arthropods ⁴ (table 1). Data collection took place during autumn 1995 on the Kiowa National Grasslands proposed Research Natural Area (RNA) in Union County, New Mexico. The RNA consists of approximately 400 acres (160 ha) of relatively flat, homogeneous shortgrass prairie that has never been plowed, though it was grazed until approximately six years ago. Collection of arthropods took place on 15, 2 ha plots spaced in a checkerboard pattern across the RNA. Average temperatures ranged from a low of 35 °F (2 °C) to a high of 70 °F (21 °C) throughout the collection dates. Post-treatment, and spring and summer collections are expected to yield even more species of arthropods.

Arthropods common to shortgrass prairie include species considered to be beneficial (i.e., pollinators, parasites, predators), as well as others that are known to cause extensive damage to

grasslands. For example, more than 1,200 insect species representing 11 taxonomic orders feed on grasses in Arizona, New Mexico, Utah, Nevada and Colorado (Thomas and Werner 1981). Grasshoppers alone regularly consume 21-23% of the annual available forage on rangelands in the western United States (Hewitt and Onsager 1983) and, in some cases, remove as much plant biomass as do domestic livestock (Swain 1943; Haws 1978). Not surprisingly, insects of southwestern rangelands are often thought of as agricultural pests because of the economically costly forage consumption by some species; however, most arthropod species are not agricultural pests, and many are beneficial components of rangeland ecosystems. In addition to serving as pollinators, arthropods are detritivores and have important roles in the decomposition of dead plant material and nutrient cycling. Furthermore, plant-feeding arthropods may even beneficially affect nutrient cycling rates (Lightfoot and Whitford 1990; Parmenter et al. 1994). Arthropods also serve as an important prey base for small mammals and birds.

Grassland burning elicits a diverse array of responses by arthropods. The degree of modification of arthropod populations by fire, the direction of change, and whether the effects are acute or chronic vary with several factors including fire characteristics, arthropod species, timing of the burn relative to phenological stage of arthropod development, influence of the fire on predator/prey and parasite/host ratios, post-burn weather, and the direction and degree of habitat restructuring (Warren et al. 1987).

One example of such interactions is the response of centipedes to fire. Centipedes feed primarily on other arthropods, and generally seek seclusion in the soil or under bark, stones or crevices of rotting logs. Although their immediate response to burning is probably minimal due to their choice of habitat, they may be affected during the recovery phase because of their dependence on other arthropods as food (Warren et al. 1987).

Preliminary results of experimental research on fire effects on predator groups of arthropods (spiders, carabid beetles, centipedes, scorpions, and solpugids) by Brantley and Parmenter (unpublished data) ⁵ indicate that there was no response to

⁴ Voucher specimens are deposited with the Museum of Southwestern Biology, Division of Arthropods, University of New Mexico, Albuquerque.

⁵ Data on file with Sevilleta LTER, New Mexico.

Table 1. Arthropods of the Proposed Research Natural Area on the Kiowa National Grasslands, Union County, New Mexico, fall 1995.

Family	Common name	Species	Authority ^a
Acrididae	Grasshoppers	<i>Ageneotettix deorum</i>	(Scudder)
		<i>Amphitornus coloradus</i>	(Thomas)
		<i>Arphia conspersa</i>	(Scudder)
		<i>Arphia pseudonietana</i>	(Thomas)
		<i>Aulocara femoratum</i>	(Scudder)
		<i>Cordillacris crenulata</i>	(Bruner)
		<i>Dactylotum b. bicolor</i>	(Thomas)
		<i>Encoptolophus sordidus</i>	(Burmeister)
		<i>Hadrotettix magnificus</i>	(Rehn)
		<i>Hesperotettix viridis</i>	(Scudder)
		<i>Hypochlora alba</i>	Dodge
		<i>Melanoplus arizonae</i>	(Scudder)
		<i>Melanoplus gladstoni</i>	Scudder
		<i>Melanoplus occidentalis</i>	(Thomas)
		<i>Melanoplus packardii</i>	Scudder
		<i>Mermiria bivittata</i>	(Serville)
		<i>Metator pardalinus</i>	(Saussure)
		<i>Opeia obscura</i>	(Thomas)
		<i>Phlibostroma quadrimaculatum</i>	(Thomas)
		<i>Phoetaliotes nebracensis</i>	(Thomas)
		<i>Spharagemon equale</i>	(Say)
		<i>Syrbula admirabilis</i>	(Uhler)
		<i>Trachyrhachys aspera</i>	Scudder
		<i>Trimerotropis pistrinaria</i>	Saussure
		<i>Tropidolophus formosus</i>	(Say)
Gryllidae	Crickets	<i>Cycloptilum comprehendens</i>	Hebard
		<i>Gryllus pennsylvanicus</i>	
		<i>Gryllus undesc.</i>	
Mantidae	Mantids	<i>Litaneutria minor</i>	(Scudder)
Rhaphidophoridae	Camel Crickets	<i>Ceuthophilus nodulosus</i>	Bruner
		<i>Ceuthophilus pallidus</i>	Thomas
Romaleidae	Lubber Grasshoppers	<i>Brachystola magna</i>	(Girard)
Tettigoniidae	Katyids	<i>Pediocetes stevensonii</i>	(Thomas)
Agelenidae	Funnel Web Spiders	<i>Agelenopsis longistylus</i>	(Banks)
		<i>Agelenopsis spatula</i>	Chamberlin & Ivie
		<i>Hololena hola</i>	(Chamberlin & Gertsch)
Gnaphosidae	Ground Spiders	<i>Drassodes gosiuta</i>	Chamberlin
		<i>Drassyllus sp.</i>	
		<i>Zelotes anglo</i>	Gertsch & Reichert
Hahniidae		<i>Neoantistea mulaiki</i>	Gertsch
Lycosidae	Wolf Spiders	<i>Hogna sp.</i>	
		<i>Pardosa sp.</i>	
		<i>Rabidosa santrita</i>	(Chamberlin & Ivie)
		<i>Schizocosa mccooki</i>	(Montgomery)
		<i>Trochosa terricola</i>	Thorell
Salticidae	Jumping Spiders	<i>Habronattus sp.</i>	
		<i>Pellenes limatus</i>	Peckham & Peckham
		<i>Phidippus sp.</i>	in revision
Philodromidae		<i>Thantus sp.</i>	

Table 1. Cont'd.

Family	Common name	Species	Authority ^a
Theridiidae	Black Widows/Comb-footed Spiders	<i>Latrodectus hesperus</i>	Chamberlin & Ivie
		<i>Steatoda sp.</i>	
Thomisidae		<i>Xysticus gulosus</i>	Keyserling
Carabidae	Ground Beetles	<i>Pasimachus californicus</i>	Chaudoir
		<i>Pasimachus elongatus</i>	(LeConte)
		<i>Pasimachus obsoletus</i>	(LeConte)
		<i>Cyclotrachelus substriatus</i>	(LeConte)
		<i>Cyclotrachelus constrictus</i>	(Say)
		<i>Dyschirius globulosus</i>	Say
		<i>Amara</i> (near) <i>idahoana</i>	
		<i>Harpalus amputatus</i>	Say
		<i>Harpalus caliginosus</i>	Fabricius
		<i>Harpalus pennsylvanicus</i>	DeGeer
Tenebrionidae	Darkling Beetles	<i>Asidopsis polita</i>	Say
		<i>Stenomorpha consors</i>	(Casey)
		<i>Stenomorpha convexicollis</i>	(LeConte)
		<i>Bothrotes plumbeus</i>	
		<i>Eleodes extricatus</i>	Say
		<i>Eleodes fusiformis</i>	LeConte
		<i>Eleodes hispilabris</i>	Say
		<i>Eleodes obscurus</i>	Say
		<i>Eleodes obsoletus</i>	(Say)
		<i>Eleodes opacus</i>	Say
		<i>Eleodes suturalis</i>	Say
		<i>Embaphion muricatum</i>	Say
		<i>Glyptasida sordida</i>	(LeConte)
		<i>Eusattus convexus</i>	LeConte
		<i>Metopoloba pruinosa</i>	Casey
Scarabaeidae	Scarab Beetles	<i>Euphoria inda</i>	(Linnaeus)
		<i>Eucanthus sp.</i>	
		<i>Paracoltalpa puncticollis</i>	LeConte
		<i>Cremastocheilus</i> (near) <i>nitens</i>	
Chrysomelidae		<i>Galeruca sp.</i>	
Cicindelidae	Tiger Beetles	<i>Cicindela scutellaria</i>	
		<i>Amblycheila cylindriformis</i>	Say
Nitidulidae	Sap Beetles	<i>Carpophilus lugubris</i>	Murray
Melyridae	Soft-winged Flower Beetles	<i>Collops quadrimaculatus</i>	Fabricius
Cleridae	Checkered Beetles	<i>Phyllobaenus sp.</i>	
Anthicidae	Ant-like Flower Beetles	<i>Baulius tenuis</i>	Casey
Melandryidae	False Darkling Beetles	<i>Anaspis rufa</i>	Say
Formicidae	Ants	<i>Crematogaster sp.</i>	
		<i>Pheidole sp.</i>	
		<i>Camponotus sp.</i>	
		<i>Pogonomyrmex occidentalis</i>	(Cresson)

^a Names in parenthesis indicate that the generic name changed since description. No parenthesis indicate original name as author described.

fire treatment. The research was conducted on the Sevilleta LTER in New Mexico. The site is a desert grassland containing many components of short-grass prairie, including blue grama and black grama. Treatment was a light burn in July 1993, with four replicates in burn treatment and control. Most of the species were able to move out of the path of the fire and recolonize the area quickly. Stronger patterns were seen in response to seasonal change than to the fire.

Other research on fire and arthropods in a prairie ecosystem include the following: fire results in increases in macroarthropod herbivores, such as white grubs and root xylem-sucking cicada nymphs (Seastedt 1984a; Seastedt et al. 1986). Only microarthropod fauna that live and feed on surface litter in tallgrass prairie exhibit declines in densities following fire (Seastedt 1984b). This response probably results more from the loss of habitat than from direct mortality (Seastedt and Ramundo 1990). True soil-dwelling microarthropods have been reported to increase in densities in response to frequent prairie fires. Higher microarthropod densities occurred in prairie areas that were more productive but had less organic matter than adjacent areas (Lussenhop 1976).

Prescribed burning may be a viable management tool against pest species of arthropods when their phenology and habits have been identified (Warren et al. 1987). For example, short-horned grasshoppers (Acrididae), the most serious grassland pests, are excellent flyers. Most short-horned grasshoppers can escape flames and quickly populate burned areas, a process that selectively favors species that are adults during the dry season when most fires occur (Gillon 1972). Spring burning in Kansas effectively controlled a few species of short-horned grasshoppers that overwinter as nymphs, but the majority of species overwinter as eggs in the soil and were not reduced when burning occurred prior to the emergence of nymphs, even after 17 consecutive annual burns (Campbell et al. 1974; Knutson and Campbell 1976). In addition, elevated post-burn soil temperatures allowed nymphs to emerge earlier than usual, which, coupled with the more nutritious vegetative regrowth, progressively increased the grasshopper population. Burning after a greater proportion of grasshopper nymphs had emerged improved control (Warren et al. 1987).

Birds

Shortgrass prairie of the southern Great Plains is used by hundreds of bird species. Many are migrants, while others breed in the Great Plains, or can be classified as summer, winter, or yearlong residents. According to newly published Breeding Bird Survey accounts, several migratory bird species that breed or winter in the southern Great Plains have declined over a 30-year period. Because birds are highly mobile, fires rarely kill birds directly, but rather affect population levels indirectly by altering habitat structure, abundance of competing species, and food levels (Bock and Bock 1990; Dickson 1981; Rotenberry et al. 1995). Some birds react to fire itself. Birds of prey in particular are attracted to fire and smoke. This positive response to fire appears to be related to vulnerability and ease of capture of prey species that are forced to flee before the flames. Several other species are attracted to recently-burned grasslands (Clark 1935; Handley 1969; Komarek 1969; Kramp et al. 1983; Lyon and Marzluff 1984; Tombak 1986). Increased forb composition and seed availability after fire is beneficial to avian herbivores and seed eaters (Bock and Bock 1990; Brock et al. 1976; Lawrence 1966; Wirtz 1977).

Other effects of fire include increased habitat heterogeneity. In shrub-grass complexes, bird diversity and abundance are enhanced if shrub cover and nesting sites are interspersed with open grassy areas maintained by fire (Baldwin 1968; Kramp et al. 1983; Pulliam and Mills 1977). Fire has also been suggested to have a cleansing effect on bird populations by lowering the numbers of parasites that affect health and vigor of individuals (Kramp et al. 1983; Lyon et al. 1978).

Many bird species that inhabit grasslands have been documented to increase habitat use in shrublands or grasslands after fire. They are reportedly attracted to smoke and flames of fire, and to recently-burned grasslands because of increased insect availability and small mammal prey vulnerability (table 2). Far fewer bird species are reported to be negatively affected by fire. These species are generally closely associated with shrubby habitat, and more abundant in unburned areas. Shrubs are required for nesting and perching, but nests are destroyed by fire, potentially reducing productivity of birds (table 2). For ex-

Table 2. Positive, negative, and mixed responses of birds of the southern Great Plains to fire events and burns based on counts, monitoring records, and anecdotal observations reported in the literature.

Species	Common Name	Response	Reference
<i>Corvus brachyrhynchos</i>	American Crow	Positive	Komarek 1969
<i>Falco sparverius</i>	American Kestrel	Positive	Bock and Lynch 1970; Lawrence 1966; Marshall 1963; Stoddard 1963
<i>Turdus migratorius</i>	American Robin	Positive	Bock and Lynch 1970; Komarek 1969; Marshall 1963; Michael and Thornburgh 1971; Roppe and Hein 1978; Stoddard 1963
<i>Ammodramus bairdii</i>	Baird's Sparrow	Positive	Madden 1995; Winter 1995
<i>Pica pica</i>	Black-billed Magpie	Positive	Komarek 1969
<i>Guiraca caerulea</i>	Blue Grosbeak	Positive	Komarek 1969
<i>Toxostoma rufum</i>	Brown Thrasher	Positive	Komarek 1969
<i>Molothrus ater</i>	Brown-headed Cowbird	Positive	Bock and Lynch 1970; Komarek 1969; Lowe et al. 1978
<i>Branta canadensis</i>	Canada Goose	Positive	Komarek 1969
<i>Corvus corax</i>	Common Raven	Positive	Lawrence 1966
<i>Gallinago gallinago</i>	Common Snipe	Positive	Komarek 1969
<i>Accipiter cooperii</i>	Coopers's Hawk	Positive	Komarek 1969; Lawrence 1966
<i>Tyrannus tyrannus</i>	Eastern Kingbird	Positive	Komarek 1969
<i>Sturnella neglecta</i>	Western Meadowlark	Positive	Komarek 1969; Lawrence 1966
<i>Sturnus vulgaris</i>	European Starling	Positive	Komarek 1969
<i>Ardea herodias</i>	Great Blue Heron	Positive	Komarek 1969
<i>Bubo virginianus</i>	Great Horned Owl	Positive	Bock and Lynch 1970; Komarek 1969
<i>Geococcyx californianus</i>	Greater Roadrunner	Positive	Marshall 1963
<i>Picoides villosus</i>	Hairy Woodpecker	Positive	Bock and Lynch 1970; Koplin 1969; Lowe et al. 1978; Taylor 1976; Taylor and Barmore 1980
<i>Eremophila alpestris</i>	Horned Lark	Positive	Komarek 1969
<i>Troglodytes aedon</i>	House Wren	Positive	Bock and Lynch 1970; Franzreb 1977; Gruell 1980; Komarek 1969
<i>Charadrius vociferus</i>	Killdeer	Positive	Komarek 1969
<i>Calamospiza melanocorys</i>	Lark Bunting	Positive	Komarek 1969
<i>Ammospiza leconteii</i>	LeConte's Sparrow	Positive	Madden 1995
<i>Lanius ludovicianus</i>	Loggerheaded Shrike	Positive	Komarek 1969
<i>Zenaida macoura</i>	Mourning Dove	Positive	Brock 1976; Bock and Lynch 1970; Komarek 1969; Lawrence 1966; Lowe et al. 1978; Soutiere and Bolen 1973; Stoddard 1963; Wirtz 1977
<i>Mimus polyglottos</i>	Northern Mockingbird	Positive	Komarek 1969
<i>Icterus spurius</i>	Orchard Oriole	Positive	Komarek 1969
<i>Buteo jamaicensis</i>	Red-Tailed Hawk	Positive	Baker 1974; Bock and Lynch 1970; Franzreb 1977; Komarek 1969; Lawrence 1966; Stoddard 1963
<i>Agelaius phoeniceus</i>	Red-winged Blackbird	Positive	Komarek 1969
<i>Passerculus sandwichensis</i>	Savannah Sparrow	Positive	Brown 1978; Daubenmire 1968; Komarek 1969; Pulliam and Mills 1977
<i>Callipepla squamata</i>	Scaled Quail	Positive	Brown 1978; Komarek 1969
<i>Anthus spragueii</i>	Sprague's Pipit	Positive	Madden 1995
<i>Tachycineta bicolor</i>	Tree Swallow	Positive	Bock and Lynch 1970; Gruell 1980; Komarek 1969; Taylor 1976; Taylor and Barmore 1980

Table 2. Cont'd.

Species	Common Name	Response	Reference
<i>Cathartes aura</i>	Turkey Vulture	Positive	Bock and Lynch 1970; Komarek 1969
<i>Sialia mexicana</i>	Western Bluebird	Positive	Franzreb 1977; Lowe et al. 1978; Marshall 1963; Szaro and Balda 1979
<i>Tyrannus verticalis</i>	Western Kingbird	Positive	Lawrence 1966
<i>Contopus sordidulus</i>	Western Wood-pewee	Positive	Bock and Lynch 1970; Komarek 1969; Lowe et al. 1978
<i>Thryomanes bewickii</i>	Bewicks's Wren	Negative	Lawrence 1966; Wirtz 1977
<i>Pipilo fuscus</i>	Brown Towhee	Negative	Lawrence 1966; Marshall 1963; Pulliam and Mills 1977; Wirtz 1977
<i>Psaltiriparus minimus</i>	Bushtit	Negative	Buttery and Shields 1975; Wirtz 1977
<i>Geothlypis trichas</i>	Common Yellowthroat	Negative	Madden 1995
<i>Ammodramus henslowii</i>	Henslow's Sparrow	Negative	Herkert and Glass 1995
<i>Ammodramus savannarum</i>	Grasshopper Sparrow	Mixed	Bock and Lynch 1970; Pulliam and Mills 1977; Madden 1995
<i>Colinus virginianus</i>	Northern Bobwhite	Mixed	Komarek 1969; Renwald et al. 1978; Thomas 1979; Wolfe 1973
<i>Sturnella magna</i>	Eastern meadowlark	Mixed	Brock et al. 1976; Komarek 1969
<i>Zonotrichia leucophrys</i>	White-crowned Sparrow	Mixed	Pulliam and Mills 1977; Taylor and Barmore 1980

ample, the shrub-associated common yellowthroat, *Geothlypis trichas*, was found to reach highest abundance on unburned areas in mixed-grass prairie, where prescribed fire has been used as a management tool for the past 20 years (Madden 1995).

Several bird species exhibit a mixed response to fire. The northern bobwhite, *Colinus virginianus*, is reportedly attracted to recently-burned grasslands and is most productive in grass-forb habitat. However, it requires scattered woody plants for cover, and populations decrease in shrub-dominated stands (Brown 1978; Komarek 1969; Kramp et al. 1983; Renwald et al. 1978; Wolfe 1973). The eastern meadowlark, *Sturnella magna*, may be attracted to recent burns, but fires that destroy all shrub cover may be detrimental (Brock et al. 1976; Komarek 1969; Kramp et al. 1983). The white-crowned sparrow, *Zonotrichia leucophrys*, depends on shrub cover, and may decrease habitat use on some burns. But it also aggregates in large groups to feed in open burns (Kramp et al. 1983; Taylor and Barmore 1980). The lark sparrow, *Chondestes grammacus*, reportedly benefits from litter removal in grasslands and reduction but not complete

removal of shrubs (Lawrence 1966; Renwald et al. 1978; Wirtz 1977).

Fire or the lack of fire may also indirectly affect birds. Several bird species, including the federally listed Species of Concern, Baird's sparrow, *Ammodramus bairdii*, grasshopper sparrow, *A. savannarum*, LeConte's sparrow, *Ammodramus leconteii*, Sprague's pipit, *Anthus spragueii*, and western meadowlark, *Sturnella neglecta*, were the most common, and abundant birds, overall, in mixed-grass prairie, where fire has been used as a habitat management tool since the 1970s, but were all completely absent from unburned prairie (Madden 1995). Baird's sparrow was found to reach high densities in areas that had been frequently burned. The areas were characterized by low litter and high cover variability of forbs and bunchgrass (Winter 1995). The decline of Montezuma quail, *Cyrtonyx montezumae*, has been linked with widespread replacement of grassland with shrubland in the last 150 years. It may benefit from fires that decrease shrub cover (Brown 1978; Kramp et al. 1983). Populations of the burrowing owl, *Athene cumicularia*, have reportedly declined on grasslands with increases in litter cover. This

suggests that the use of fire to reduce litter cover may be beneficial to this species (Komarek 1969; Kramp et al. 1983). The lesser prairie-chicken, *Tympanuchus pallidicinctus*, is also a grassland species reported to be declining in the Southwest because of decreased grassland habitat due to suppression of rangeland fires (Brown 1978). Regrowth of grasses, reduced litter, and decreased shrub cover in grasslands following fire is beneficial for the Sandhill crane, *Grus canadensis*, a common grassland migrant (Kirsh and Kruse 1973; Kramp et al. 1983).

Herpetofauna

There is a general paucity of data on the response of reptiles and amphibians to fire in grasslands. See Scott (this volume) for a discussion of herpetofauna and fire in grasslands.

Mammals

The reaction of mammals to fire is a function of size and vagility. Deer and elk easily avoid injury during fire (Boeker et al. 1972; McCulloch 1969; Dills 1970; Hallisey and Wood 1976), although young ungulates are frequently killed by large fires (Daubenmire 1968; Kramp et al. 1983). Most small mammals escape fires by hiding in burrows or rock crevices (Howard et al. 1959; Heinselman 1973). Komarek (1969) observed that mature cotton rats successfully moved themselves and their young to safe refuge areas. Thus, even small mammals of limited mobility are capable of avoiding fire (Kramp et al. 1983).

The most common cause of death for small mammals during fire is a combination of heat effects and asphyxiation. However, studies cited by Bendell (1974) indicate that soil provides insulation from fire for burrowing animals (Kramp et al. 1983). Other causes of death include physiological stress as mammals overexert themselves to escape, trampling as large mammals stampede, and predation as small mammals flee from fire (Kaufman et al. 1990).

Grassland fires that temporarily remove food and cover (litter and standing dead vegetation) may be detrimental to small rodents immediately after fire (Daubenmire 1968; Kaufman et al. 1990). However, repopulation of such areas is reported to

be nearly complete within 6 months (Cook 1959). Mice and rodent populations often increase after fire in response to increased availability of forb seeds and insects (Lyon et al. 1978). In addition, burned areas often support more diverse animal populations than comparable unburned sites due to increased habitat diversity (Beck and Vogl 1972; Wirtz 1977). Omnivores and carnivores are attracted to burns by increased plant diversity and associated small mammal populations (Gruell 1980). Levels of animal parasites are often lower in burned habitats (Bendell 1974).

Kaufman et al. (1990) suggest that most effects of fire on small mammals in grasslands are not neutral, but are instead either fire-positive or fire-negative responses. Fire-negative mammals include species that forage on invertebrates in the litter layer, species that live in relatively dense vegetation and eat plant foliage, and species that use, at least partially, aboveground nests of plant debris. Examples in the southern Great Plains include the cotton rat, *Sigmodon hispidus*, Bailey's pocket mouse, *Perognathus baileyi*, the pinyon mouse, *Peromyscus truei*, the white-tailed antelope ground squirrel, *Ammospermophilus leucurus*, the southern red-backed vole, *Clethrionomys gapperi*, the white-throated woodrat, *Neotoma albigula*, the western harvest mouse, *Reithrodontomys megalotis*, and the meadow vole, *Microtus pennsylvanicus* (Beck and Vogl 1972; Bock and Bock 1978; Brock et al. 1976; Bradley and Mauer 1973; Geier and Best 1980; Hanson 1978; Kaufman et al. 1990; Komarek 1969; Kramp et al. 1983; Lawrence 1966; Lowe et al. 1978; Mazurek 1981; Rowe and Scotter 1973; Taylor 1969).

Fire-positive mammals include species that use ambulatory locomotion in microhabitats with a relatively open herbaceous layer and feed on seeds and/or insects and that use saltatorial locomotion (Kaufman et al. 1990). They exhibit an increase in populations and habitat use after fire because of an increased availability of forb seeds, insects, newly greening vegetation, the creation of open areas in otherwise dense habitat, and eventually an increase in forb cover. Increases may occur immediately, or gradually as the areas begin to revegetate and habitat diversity increases. The small mammals include the deer mouse, *Peromyscus maniculatus*, the white-footed mouse, *Peromyscus leucopus*, the eastern cottontail, *Sylvilagus*

floridanus, Merriam's kangaroo rat, *Dipodomys merriami*, (*Dipodomys ordii* occurs in the southern Great Plains), the southern grasshopper mouse, *Onychomys torridus*, (*Onychomys leucogaster* occurs in the southern Great Plains), Nuttall's cottontail, *Sylvilagus nuttallii*, the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*, and the hispid pocket mouse, *Chaetodipus hispidus* (Beck and Vogl 1972; Bradley and Mauer 1973; Cable 1967; Cook 1959; Daubenmire 1968; Heinselman 1973; Kaufman et al. 1990; Komarek 1969; Kramp et al. 1983; Lawrence 1966; Lowe et al. 1978; Roppe and Hein 1978; Thomas 1979; Williams 1955).

Carnivores that occur in the southern Great Plains include badger, *Taxidea taxus*, bobcat, *Felis rufus*, red fox, *Vulpes vulpes*, and coyote, *Canis latrans*. These species may increase habitat use in response to fire-enhanced rodent populations (prey) (Gruell 1980; Kramp et al. 1983; Wirtz 1977).

Most native ungulates, including buffalo, *Bison bison*, white-tailed deer, *Odocoileus virginianus*, elk, *Cervus elaphus*, and pronghorn, *Antilocapra americana*, increase in population and habitat use after fire. The response is due to an increase in forage quality and quantity in newly burned areas. Deer have also been observed eating ash after a fire, possibly for the concentrated mineral content (Baldwin 1968; Basile 1979; Boeker et al. 1972; Carpenter et al. 1979; Davis 1977; Dills 1970; Ffolliott et al. 1977; Gruell 1980; Hallisey and Wood 1976; Hendricks 1968; Keay and Peck 1980; Kirsh and Kruse 1973; Kittams 1973; Komarek 1969; Kramp et al. 1983; Kruse 1972; Leege and Hickey 1971; Leege 1968; Leopold 1923; Lowe et al. 1978; McCulloch 1969; Miller 1963; Nelson 1974; Pederson and Harper 1978; Reynolds 1969; Roppe and Hein 1978; Rowe and Scotter 1973; Short 1977; Short et al. 1977; Wallmo et al. 1977).

TIMING AND FREQUENCY OF FIRE

Grassland communities are likely to be influenced by seasonality and frequency of fire due to their evolutionary adaptations to particular habitat features and conditions. In many areas, however, effects of different fire regimes remain poorly understood and, where important conservation or management issues are involved, controversial (Glitzenstein et al. 1995).

Summer fires can stimulate seed yields of native grasses more than fires in winter or early spring (Biswell and Lemon 1943; Patton et al. 1988). Variability in the population dynamics of some plant species appear to be related largely to variation in fire behavior (intensity, percent of area burned, fuel consumption), regardless of the season of burning, while other plant species are least vulnerable to dormant-season burning and most vulnerable to burning early in the growing season (Glitzenstein et al. 1995). In general, plant species in semi-arid grasslands are more strongly influenced by fire season and frequency than behavior (Steuter and McPherson 1995). Responses of arthropods to season and frequency of fire also appear to vary by species (Warren et al. 1987).

Birds, in general, are most vulnerable to fire during nesting and fledging periods. Fires can be devastating to ground-nesting birds because they destroy existing nests, remove protective cover and eliminate insect food resources (Daubenmire 1968) that may be associated with ground litter and vegetation. Therefore timing of prescribed burns should be a major consideration to resource managers concerned with declining populations that breed in the southern Great Plains. The effects of seasonal prescribed burns in Florida prairies on the federally endangered Florida grasshopper sparrow, *Ammodramus savannarum floridanus*, and Bachman's sparrow, *Aimophila aestivalis*, were experimentally examined. Even though endangered species management for the Florida grasshopper sparrow was focused on the concept of winter season burns, both species were found to respond favorably to summer burns (Shriver and Vickery 1995).

No studies have focused on the issue of seasonal effects of fire on small mammals. Since most of the effects of season on population responses will undoubtedly be more subtle than general fire-negative and fire-positive responses, studies of differences in effects of grassland fires on small mammal populations will require intensive, replicated studies (Kaufman et al. 1990). Numerous studies have examined the response of small mammals in spring and autumn or spring and winter burn plots (Bock and Bock 1978, 1983; Bock et al. 1976; Tester and Marshall 1961); however, due to lack of replicates, no effects of season were evident, and these analyses focused on only the

general effects of fire on small mammals (Kaufman et al. 1990).

CONCLUSION

The effects of fire on animal community structure in grasslands are related to trophic relationships and plant community structure (i.e., amount of litter, shrub, and grass cover). Conceivably, the effects of fire on arthropods will carry over to birds and small rodents that rely on arthropods as their prey base. This in turn will affect larger mammals and raptors. These relationships change rapidly as vegetation establishes and grows in recently-burned areas. Thus, community structure is likely to be temporally dynamic. Change is the normal course of events for most ecological systems (Connell and Sousa 1983). Management of ecosystems is challenging in part because we seek to understand and manage areas that change (ESA 1995).

Knowledge of plant and animal response to fire timing and frequency should allow scientists and resource managers to predict the effects of prescribed burns on ecosystems. For example, prescribed fire in prairie in Illinois eliminated the federally listed Species of Concern, Henslow's sparrow (*Ammodramus henslowii*) from burned areas. Data suggest that Henslow's sparrows relocate to adjacent unburned areas of prairie when their preferred areas were burned. Because of the species sensitivity to prescribed fire, it was recommended by the Illinois Endangered Species Protection Board that managers of prairies where this species occurs use a rotational system of burning in which no more than 20-30% of the site is burned in any year (Herkert and Glass 1995).

Research Needs

Most previous research on the effects of fire on plant and animal communities in shortgrass prairie has not employed the experimental approach, but has instead relied on study designs that are largely descriptive in nature. Descriptive research is suitable for identifying patterns, but is considerably less useful for determining underlying mechanisms. This type of research has limited predictive power, and consequently, limited utility

to managers. Thus, although descriptive research has generated many hypotheses about ecological phenomena, few of these hypotheses have actually been tested (Weltzin and McPherson 1995). Manipulative field-based experimental research will help disentangle important driving variables because of strong correlations between factors under investigation (Gurevitch and Collins 1994). Identification of underlying mechanisms of change in community structure will enable us to predict community response to changes in driving variables (e.g., climate change, or fire) with a level of certainty useful to management. Some examples of research needs that can be addressed with experiments are the evaluation of the population responses of arthropods and vertebrates to prairie restoration using prescribed fire; identification of plant and animal species that are fire-dependent, neutral, or exhibit positive or negative responses to fire; evaluation of length of time after fire before positive or negative responses are produced; evaluation of the use of prescribed fire to benefit sensitive, threatened, or endangered plant and animal species; and, determination of whether fire suppression, or differences in season and frequency of prescribed burns will continue to contribute to population declines of some species.

Some important questions can be addressed only at spatial scales may be incompatible with experimentation. These include the assessment of prescribed fire to create desirable landscape patterns for managing populations of plant and animal species, such as game animals, endangered species, neotropical migratory birds, and other featured species; landscape and regional analysis of patterns of species endangerment and abundance in relation to quantity and configuration of vegetation type and structure; and modeling of fire use to reverse undesirable trends in sizes of populations and habitats.

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Evolution and management of the North American grassland herpetofauna

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Abstract.—The modern North American grassland herpetofauna has evolved in situ since the Miocene. Pleistocene glaciation had a minimal effect except in the far North, with only minor displacements of some species. South of the glaciers, winters were warmer and summers cooler than at present. Snake-like reptiles, leaping frogs, and turtle “tanks” are favored adaptive types in uniform dense grassland. A typical fauna consists of about 10-15 species, mostly snakes. Special habitat components, such as streams and ponds, bare ground, sand, trees, prairie dog towns, and rocky outcrops, add distinct suites of species. There is also an increase in species number from north to south and west to east. Grassland use and management, such as prairie dog control, off-road vehicle traffic, and brush removal, have demonstrable effects on the herpetofauna. However, the effects of three of the most widespread management procedures—water development, grazing, and fire—are largely unstudied. Although highly fragmented, the majority of species of grassland reptiles and amphibians are widespread and populations are resilient, but there are special conservation problems associated with Pleistocene relicts with limited distributions.

INTRODUCTION

At the time of the arrival of Europeans in North America, much of the interior of the continent was covered by grasslands. The heart of this great expanse was the tallgrass prairie of the midwestern United States. Where they were not bounded by mountain massifs, the lush grasslands feathered off to shortgrass prairies and desert grasslands in the west and south, shortgrass prairie and coniferous parklands and forests in the north, and deciduous forests in the east. The original grasslands and their accompanying faunas were continuously distributed, with few biogeographic barriers. With the westward expansion of European-style agriculture, most of the prairie was rapidly and completely converted to agriculture, producing a highly fragmented biota.

Parmenter et al. (1994) documented the exceptionally high vertebrate diversity in southwestern rangelands, and they emphasized that preservation of this biodiversity in the remaining habitat fragments will depend on skillful management of human activities in a fashion that integrates faunal biology, resource requirements, and historic movement patterns.

Nongame species, especially reptiles and amphibians, are not usually accorded the attention in land management decisions that their proportionate contribution to local biodiversity deserves. The situation has not changed much in the last 15 years (Bury et al. 1980); one of the few grassland management programs focused explicitly on reptiles or amphibians is the bullsnake (*Pituophis melanoleucus*) control trapping that has been carried out for decades at Valentine National Wildlife Refuge in Nebraska (Imler 1945). As a partial remedy, this review is intended to explore the characteristics of grassland herpetofaunas, to

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examine the issues involved in their management, and to make recommendations for managers concerned with enhancing the herpetological components of the remaining prairie fragments need to accomplish this important task. I will explore several areas:

- The history of the grassland herpetofauna
- The adaptations and habitats of grassland reptiles and amphibians
- The management of grassland reptiles and amphibians
- Conservation concerns
- Management recommendations

HISTORY OF THE GRASSLAND HERPETOFAUNA

Is there a coevolved North-American grassland herpetofauna?

Savage (1960) recognized a modern North American desert and plains herpetofauna whose boundaries are determined by zones of relatively rapid species transitions into different surrounding herpetofaunas (fig. 1). The present study deals with this herpetofauna, which inhabits the entire mid-continental grassland, including the Sonoran and Chihuahuan desert grasslands and the Great Basin. The grassland herpetofauna includes all of the reptiles and amphibians inhabiting this area, not just those that live in the grass. My conclusions are specific to the area; they often do not apply to grasslands outside of the area, such as the Central Valley of California, that have been long isolated from the grasslands in the central core of North America.

With the increasingly xeric climate of the late Miocene, the modern, unbroken grasslands began to form by coalescence of previously scattered and isolated fragments (Axelrod 1985). In marked contrast to mammalian faunas that experienced massive Pleistocene extinctions, North American herpetofaunas have changed remarkably little since the Pliocene. Pleistocene herpetofaunas from western North America were composed of most of the same species that are found there now (Holman 1995; Rogers 1982; Parmley 1990). The major difference stems from the loss of several



Figure 1. Distribution of the modern North American desert and plains herpetofauna. After Savage (1960).

tortoises of the genus *Geochelone* (Moodie and Van Devender 1979). Representatives of this ancient, worldwide radiation of medium to giant-sized tortoises were present in many fossil North American grassland faunas throughout the Tertiary. Members of the genus are still found in many parts of the tropics, but they are now extinct in North America. Based on well-documented fossil evidence, the Great Plains herpetofauna evolved in situ since at least the Miocene, with only minor east-west and north-south shifts that coincide with Pleistocene glaciations. Historic stability has produced a recognizable grassland herpetofauna that is relatively uniform across the North American plains.

The patterns of modern herpetofaunal diversity were accomplished mainly by the addition or deletion of species from a widespread suite of grassland forms. Most species are wide-ranging, supporting the notion that the grassland fauna is fairly homogeneous. For example, half (6 of 12) of the reptile and amphibian species found in the grasslands of Alberta and almost three-fourths (32 of 43) of the Kansas tallgrass species are also found in the grasslands of Chihuahua, several hundred kilometers to the south (Morafka 1977; Collins 1993; Russell and Bauer 1993).

What were the ecological conditions under which the herpetofauna evolved?

The presence of *Geochelone* in the fossil record of the midwestern United States from the Oligocene through the last glaciation (about 10,000 years ago) is especially enlightening (Moodie and Van Devender 1979). At the same time that *Geochelone* became extinct in North America, the ranges of four species of grassland tortoises of the genus *Gopherus* contracted into western, eastern and southern enclaves, where they survive to the present day (fig. 2). Moodie and Van Devender (1979) attributed these extinctions and range reductions to post-Pleistocene climatic deterioration, perhaps assisted by human predation. The fossil presence in Kansas of *Geochelone*, which is not known to dig burrows, was taken to indicate a climate that was essentially frost-free. Later, *Geochelone* died out, whereas *Gopherus* has survived at the southern and western edges of its Pliocene distribution probably because of its ability to escape predators and freezing temperatures by burrowing (Holman 1971, 1980; Moodie and Van Devender 1979; Rogers 1982).



Figure 2. Modern distributions of three gopher tortoises (*Gopherus*; hatching and stipple) and late Pleistocene fossil localities for *Gopherus* and *Geochelone* (dots). After Moodie and Van Devender (1979).

The combined paleontological evidence from vertebrates, plants, and mollusks indicates that climates with cooler summers, milder winters, and possibly more precipitation prevailed in unglaciated North America until modern climatic patterns were established about 10,000 years ago (Holman 1995; Wright 1987). Climates south of the glaciers were relatively immune to the alternating glacial and interglacial cycles (Holman 1995). Bryson and Wendland (1967) hypothesized that the immense Pleistocene glaciers prevented the southward incursion of Arctic air masses that now bring sub-zero temperatures to most of the continent, and Rogers (1982) attributed the cooler summers and warmer winters to a greenhouse effect with heavy cloud cover and increased moisture. Under these conditions, the grassland herpetofauna has persisted largely intact to the present day.

ADAPTATIONS AND HABITATS OF GRASSLAND REPTILES AND AMPHIBIANS

What are the adaptive characteristics that enable reptiles and amphibians to live in grasslands?

We can gain some insight into the adaptations that allow reptiles and amphibians to inhabit grasslands by looking at their common characteristics. This is admittedly a speculative, circular process (if a grassland species has a trait, then that trait is an adaptation to grasslands), but some of the speculation will be useful, especially in those cases where we can identify a context in which the "adaptation" could operate.

The most common adaptive traits seen in grassland reptiles are leglessness and serpentine locomotion as seen in snakes and smooth, legless (or small-limbed) lizards (table 1). Legs are a liability when a serpentine reptile is threading its way between dense grass stems, and lizards that depend on their legs for locomotion are most common in grasslands where there are openings, such as rocky outcrops, tree trunks, or bare ground. As we shall see in the next section, the adaptive type exemplified by snakes appears to be very successful at exploiting uniform grasslands.

Frog locomotion seems to be another good way to negotiate grasslands. Grassland frogs have

Table 1. Adaptive types of reptiles and amphibians present in various North American grasslands. Figures in the table are the number of species and (percentages) of each adaptive type in the total terrestrial grassland herpetofauna in that area. "Toads" includes all dry, short-legged, hopping anurans that are resistant to desiccation (Bufonidae, Leptodactylidae, Microhylidae, Pelobatidae); "Frogs" includes moist, long-legged, leaping anurans that dry up easily (Ranidae, Hylidae); and "Snakes" includes snakes and legless lizards (Anguidae) that move by serpentine locomotion.

Adaptive type	Tallgrass Kansas ¹	Great Basin Western Utah ²	Southern Desert Chihuahua, Coahuila ³	Northern Southern Alberta ⁴
Salamanders	1 (2.3)	0 (0.0)	1 (1.8)	1 (8.3)
"Toads"	7 (16.3)	2 (9.5)	9 (16.4)	3 (25.0)
"Frogs"	4 (9.3)	1 (4.8)	1 (1.8)	2 (16.7)
Turtles	2 (4.7)	0 (0.0)	4 (7.3)	0 (0.0)
Lizards	7 (16.3)	9 (42.9)	18 (32.7)	1 (8.3)
"Snakes"	22 (51.2)	9 (42.9)	22 (40.0)	5 (41.7)
# of Species	43	21	55	12

¹ Collins 1993

² Stebbins 1985

³ Morafka 1977

⁴ Russell and Bauer 1993

exceptionally powerful, high-arched leaps that enable them to clear the top of the grassy barrier. A third successful type of locomotion in dense grasslands is "tank" locomotion, by which turtles are able to force their way through small gaps between grass clumps.

Many bodies of water in grasslands are ephemeral, generally filling in the winter and spring, and drying during the summer and fall. Therefore, many of the most successful amphibians are species that have relatively short aquatic larval stages.

What characteristics of grassland habitats are correlated with reptile and amphibian species diversity?

The tallgrass prairie of the eastern Great Plains is the simplest and most uniform of the grassland habitats. About 15 reptile species (mostly snakes) can be present in an undifferentiated tallgrass prairie in Kansas (table 2). Long-limbed lizards, several toad species, and a snake are able to use the grasslands in places where bare ground gives them the freedom to move about rapidly, allowing them to forage and escape effectively. The simple addition of temporary water sources can add up to seven species of amphibians, a turtle and three

snakes. Sandy or other loose, friable soil is necessary for species that dig. Rocky soils provide hiding places for small snakes, and rocky outcrops and trees provide elevated perches where collared (*Crotaphytus*) and prairie lizards (*Sceloporus*) can display. Rivers and large streams and their associated riparian zones finger out into the Great Plains from the east and south, bringing to the grasslands a series of frogs, turtles, and snakes that have their centers of distribution in the eastern United States.

As one moves west from Kansas tallgrass prairie toward the Great Basin, the grasslands become more open, tending to favor lizard species. On the other hand, they become drier, which diminishes the number of snakes, turtles, and amphibians. Total herpetofaunal species richness is halved, but the number of lizard species actually increases (table 1). Southward into the Chihuahuan Desert grasslands, the percentage of lizard species doubles and frogs decline, but overall species richness increases by about 25% with the addition of tropical "toads," turtles, and lizards (Morafka 1977; Van Devender and Bradley 1994). Northward into Alberta, species richness decreases dramatically, but the percent composition of different adaptive types remains roughly similar to that in Kansas.

Table 2. List of reptiles and amphibians in Kansas grasslands and their habitat correlates. Data from Collins (1993).

Common name	Scientific name	Common name	Scientific name
Inhabitants of undifferentiated grasslands		Inhabitants of sandy soils	
Ornate box turtle	<i>Terrapene ornata</i>	Glossy snake	<i>Arizona elegans</i>
Great Plains skink	<i>Eumeces obsoletus</i>	Western hognose snake	<i>Heterodon nasicus</i>
Prairie skink	<i>Eumeces septentrionalis</i>	Inhabitants of sandy soils and water	
Western slender glass lizard	<i>Ophisaurus attenuatus</i>	Woodhouse's toad	<i>Bufo woodhousei</i>
Racer	<i>Coluber constrictor</i>	Inhabitants of trees or rocks	
Western rattlesnake	<i>Crotalus viridis</i>	Eastern collared lizard	<i>Crotaphytus collaris</i>
Ringneck snake	<i>Diadophis punctatus</i>	Prairie lizard	<i>Sceloporus undulatus</i>
Night snake	<i>Hypsiglena torquata</i>	Great Plains rat snake	<i>Elaphe guttata</i>
Prairie kingsnake	<i>Lampropeltis calligaster</i>	Milk snake	<i>Lampropeltis triangulum</i>
Common kingsnake	<i>Lampropeltis getula</i>	Ground snake	<i>Sonora semiannulata</i>
Texas blind snake	<i>Leptotyphlops dulcis</i>	Plains black-headed snake	<i>Tantilla nigriceps</i>
Gopher snake	<i>Pituophis melanoleucus</i>	Inhabitants of rocky canyons and water	
Long-nosed snake	<i>Rhinocheilus lecontei</i>	Red-spotted toad	<i>Bufo punctatus</i>
Massasauga	<i>Sistrurus catenatus</i>	Inhabitants of rivers, riparian zones, or permanent ponds	
Lined snake	<i>Tropidoclonion lineatum</i>	Cricket frog	<i>Acris crepitans</i>
Inhabitants of temporary water		Bullfrog	<i>Rana catesbeiana</i>
Tiger salamander	<i>Ambystoma tigrinum</i>	Snapping turtle	<i>Chelydra serpentina</i>
Red-spotted toad	<i>Bufo punctatus</i>	Painted turtle	<i>Chrysemys picta</i>
Great Plains narrowmouth toad	<i>Gastrophryne olivacea</i>	Red-eared slider	<i>Trachemys scripta</i>
Spotted chorus frog	<i>Pseudacris clarki</i>	Smooth softshell turtle	<i>Trionyx muticus</i>
Boreal chorus frog	<i>Pseudacris maculata</i>	Spiny softshell turtle	<i>Trionyx spiniferus</i>
Western chorus frog	<i>Pseudacris triseriata</i>	Eastern hognose snake	<i>Heterodon platirhinus</i>
Plains leopard frog	<i>Rana blairi</i>	Plain belly water snake	<i>Nerodia erythrogaster</i>
Yellow mud turtle	<i>Kinosternon flavescens</i>	Diamondback water snake	<i>Nerodia rhombifer</i>
Checkered garter snake	<i>Thamnophis marcianus</i>	Northern water snake	<i>Nerodia sipedon</i>
Plains garter snake	<i>Thamnophis radix</i>	Graham's crayfish snake	<i>Regina grahamii</i>
Common garter snake	<i>Thamnophis sirtalis</i>	Brown snake	<i>Storeria dekayi</i>
Inhabitants of bare ground		Western ribbon snake	<i>Thamnophis proximus</i>
Six-lined racerunner	<i>Cnemidophorus sexlineatus</i>	Inhabitants of bare ground and water	
Lesser earless lizard	<i>Holbrookia maculata</i>	Great Plains toad	<i>Bufo cognatus</i>
Texas horned lizard	<i>Phrynosoma cornutum</i>	Green toad	<i>Bufo debilis</i>
Coachwhip	<i>Masticophis flagellum</i>	Plains spadefoot toad	<i>Spea bombifrons</i>

THE MANAGEMENT OF GRASSLAND REPTILES AND AMPHIBIANS

What management tools are available and what are their effects on grassland reptiles and amphibians?

Given the common components of all of the grassland herpetofaunas, general management principles often can be applied over wide areas (Table 3).

Water management

Water manipulation for the enhancement of livestock grazing and agriculture is ubiquitous in grasslands. Devices used range from bulldozer scrapes and check dams that temporarily store runoff and extend the grazing season, to complex

systems that include permanent reservoirs behind high dams, ditches, channeled streams, and eradication of phreatophytes (Elmore and Kauffman 1994).

All grassland amphibians require water for the development of their larvae. The great majority of species use temporary ponds that hold water for at least several months in spring and summer and not streams or rivers. At one time, buffalo wallows probably provided temporary pond habitats in many grasslands, but these have largely disappeared. The suitability of a pond for amphibians is tightly tied to the duration of its water cycle: If ponds dry up too soon, larvae will die; if they last too long, predatory mammals, aquatic insects, and even fish will become abundant.

Ponds that contain water much of the year attract mammalian predators such as opossums (*Didelphis*), coyotes (*Canis*), foxes (*Vulpes*), badgers (*Taxidea*), skunks (*Mephitis*), and raccoons (*Pro-*

Table 3. Effects of management techniques on grassland herpetofaunas.

Management practice	Positive effects	Negative effects
Creation of temporary ponds ¹	Habitat for native amphibians and mud turtle	Increase in mammalian predators
Provision of permanent water ²	Habitat for aquatic turtles, snakes, bullfrogs	Addition of many terrestrial and aquatic vertebrate predators
Moderate grazing ³	Increases lizard species diversity?	Unknown
Heavy grazing ³	Some lizards densities increase	Some lizards decrease; some lizard species lost
Brush removal ⁴	Some lizard populations increase	Most lizards decline, some species lost, tortoises decline
Grass planting ⁵		Most lizards decline, some species lost?
Burning ⁶		Box turtles burned
Prairie dog control ⁷		Rattlesnakes, earless lizards decline
Off-road vehicles ⁸		Fewer lizards

¹ Personal observation

² Moyle 1973, Hayes & Jennings 1986, Schwalbe & Rosen 1989

³ Jones 1981

⁴ Busack and Bury 1974, Berry 1978, Germano and Hungerford 1981, Rose and Judd 1982, H.L. Snell (personal communication)

⁵ The effects of exotic grass introductions on herpetofaunas have not been studied, but Bock et al. (1983) and D'Antonio and Vitousek (1992) discuss impacts on other elements of the grassland biota

⁶ Bigham et al. 1965, Erwin and Stasiak 1979

⁷ Klauber 1972, Miller et al. 1990

⁸ Busack and Bury 1974, Vollmer et al. 1976, Bury et al. 1977

cyon). Christiansen and Gallaway (1984) increased the hatchling recruitment of seven species of turtles three to four fold by removing raccoons from the vicinity of an Iowa pond. Recruitment declined again after raccoons became reestablished.

Ponds that hold water the entire year, year after year, have ecological consequences distinct from those of temporary ponds. Permanent water provides habitat for the bullfrog (*Rana catesbeiana*) plus a number of fishes, snakes, and turtles that usually only penetrate the grasslands along permanent streams and rivers. The introduction of fish, especially predatory centrarchids and catfish, and bullfrogs has been implicated in the disappearance of native species in several places (Moyle 1973; Hayes and Jennings 1986; Schwalbe and Rosen 1989; Collins et al. 1989).

Ponds that enhance grasslands for amphibians and reptiles need not be sophisticated. A simple scrape that collects and holds spring rain water and snow melt through July is sufficient for many species. Ponds that are fenced from livestock are often more attractive to reptiles and amphibians because they usually have a better cover of emergent aquatic and riparian plants. Cows also degrade the banks and eventually churn a shallow pond into a muddy morass (personal observation).

Livestock grazing

Livestock grazing is the most widespread human-mediated influence on grassland vegetation in the American West (Fleischner 1994 and references therein). In addition to the direct effects of grazing, management of grasslands for cattle often includes brush and tree clearing and planting exotic grasses. Vegetative structure has been shown to affect North American lizard communities in predictable ways (Pianka 1966; Germano and Lawhead 1986), but nothing is known about the responses of other reptiles and amphibians. In many North American grasslands and savannas, grazing has been implicated in the invasion of woody vegetation and non-native grasses; in others, especially riparian zones, shrubs and trees are suppressed or eliminated by grazing livestock (D'Antonio and Vitousek 1992; Vavra et al. 1994 and references therein). The removal of riparian

vegetation and the mechanical destruction of stream and pond banks by cows and sheep can have a significant detrimental effect on the herpetofauna (Szaro et al. 1985; Jones 1989).

In dense grasslands, moderate grazing can increase vegetative patchiness and structure, opening up areas for use by widely-foraging lizards, snakes, and even toads. In drier, more open grassland formations, grazing effects are less predictable. Heavy grazing can reduce patchiness and promote homogeneity, which may benefit a few species of essentially desert lizards (Busack and Bury 1974), but it can also facilitate the invasion of brush and trees, which provide habitat for arboreal species at the expense of widely-foraging terrestrial lizards (Jones 1981). In southern Texas, heavy grazing favors the growth of prickly pear (*Opuntia*) which is a staple in the diet of the Texas tortoise (*Gopherus berlandieri*, Auffenberg and Weaver 1969). Claims that competition for food and mechanical injury by livestock have had a detrimental effect on Mojave Desert tortoise (*Gopherus agassizii*) populations may be true (Woodbury and Hardy 1948; Berry 1978; Coombs 1979; Nicholson and Humphreys 1981; Campbell 1988), but they are disputed (Bostick 1990) and have not been tested (Oldemeyer 1994).

Brush removal

Brush removal simplifies habitat structure, benefiting some reptile and amphibian species and eliminating others. The removal of competing shrubs allows grass to proliferate. Rose and Judd (1982) believe that brush clearing in southern Texas is detrimental to tortoise populations, but Auffenberg and Weaver (1969) think that the damage is short-term, and that tortoise habitat is ultimately enhanced by the practice because grass is encouraged. Partial removal of mesquite (*Prosopis juliflora*) in an Arizona grassland changed the proportions of the lizard species, but the species present and total numbers remained about the same; complete mesquite removal reduced the number of lizards by more than 50% and three common species virtually disappeared (Germano and Hungerford 1981). Increased grass density on the mesquite-free plot was suggested as the reason for the disappearance of some of the widely-

foraging lizard species. In a depauperate reptile fauna in Great Basin grasslands of eastern Oregon, Werschkul (1982) found lizards in all habitats with shrubs or rocky outcrops; he saw no lizards in grasslands that had been "restored" and lacked woody vegetation. In New Mexico, populations of the dune lizard (*Sceloporus arenicolus*) were reduced by 70-94% in areas where shinnery oak (*Quercus harvardii*) was removed (H.L. Snell personal communication). Invasion of the treated areas by dense stands of grasses and forbs was thought to be the main reason for the disappearance of the dune lizards.

Grass plantings

Aside from the accidental introduction of exotic grasses into sensitive native grasslands, at least three invasive, non-native perennial grasses are being planted as livestock forage in different parts of the North American grasslands (D'Antonio and Vitousek 1992). The effects of these plantings on the herpetofauna have not been studied in any detail, but many lizards, especially *Uta*, *Holbrookia* and *Cnemidophorus*, seem to be sensitive to grass clogging their foraging, display, and escape pathways (Germano and Hungerford 1981 personal observation).

Eurasian crested wheatgrass (*Agropyron desertorum*) has been widely planted throughout the Great Basin as a drought-tolerant replacement for the native *A. spicatum* (D'Antonio and Vitousek 1992, Rogler and Lorenz 1983).

Buffelgrass (*Cenchrus ciliaris*) is planted for cattle forage in the lower Rio Grande Valley of southern Texas and northeastern México, and in the Sonoran Desert (Nabham 1994; Warren 1994). The grass is very successful at colonizing open ground between mesquite and ironwood (*Olneya tesota*) trees. Two species of lizards that depend on open spaces and running for foraging and escape, the reticulate collared lizard (*Crotaphytus reticulatus*) and the spot-tailed earless lizard (*Holbrookia lacerata*), are restricted to the lower Rio Grande Valley. Buffelgrass clogs their habitat, rendering it unsuitable (A.H. Price personal communication).

A similar, and perhaps more widespread, problem is occurring with the widespread use of African Lehmann's lovegrass (*Eragrostis*

lehmanniana) in many parts of southeastern Arizona and southern New Mexico. Lovegrasses have been shown to diminish or eliminate many native populations of plants, birds, rodents, and grasshoppers (Bock et al. 1986).

Burning

Herpetofaunal responses to burning of North American grasslands have scarcely been studied. Box turtles (*Terrapene ornata*, *T. carolina*) seem to suffer fairly heavy losses in some situations, but other reptile populations are hardly affected. After an August fire on a 160 ha pasture in eastern Oklahoma, Bigham et al. (1965) found 25 dead and three live box turtles, a dead rattlesnake (*Crotalus* sp.), a dead copperhead (*Agkistrodon contortrix*), a live black rat snake (*Elaphe obsoleta*), and a live coachwhip snake (*Masticophis flagellum*). Erwin and Stasiak (1979) looked for dead animals in a 65 ha restored prairie in three successive springs after controlled burns. They found dead snakes after one of the fires: a bullsnake and two garter snakes (*Thamnophis radix*, *T. sirtalis*). Four live snakes were also seen. Legler (1960) assumed that ornate box turtles (*Terrapene ornata*) were occasionally killed by prairie fires, but he found no carcasses after an early April fire on his study plot. Two years later, he did find a large female box turtle that had been badly scarred by fire.

Mushinsky (1985) found that regular fires in Florida sandhills increased herpetological diversity and abundance, especially populations of the six-lined racerunner (*Cnemidophorus sexlineatus*). The intensity, timing, and frequency of burning help determine the structure of the vegetation, and lizard communities, especially, should be affected. Bury and Smith (1986) recommended small control burns to open up shrub grasslands for Texas tortoises in south Texas.

Prairie dog control

Because prairie dogs (*Cynomys* spp.) theoretically compete with livestock for forage, their eradication is a time-honored management practice among western ranchers (Miller et al. 1990). Eradication has been very effective; it is estimated

that prairie dogs persist on only about 2% of their former range (Ceballos et al. 1993; Miller et al. 1994). Nonetheless, a recent cost/benefit analysis concluded that prairie dog control programs operate at a net economic loss, even if the effects on non-target species, such as the black-footed ferret (*Mustela nigripes*), or the prairie dog's role in soil formation and nutrient cycling are not considered (Collins et al. 1984; Miller et al. 1990; Sharps and Uresk 1990; Samson and Knopf 1994).

Prairie dogs are "keystone" species in their ecosystem, and their towns have been called species diversity oases on the arid plains (Miller et al. 1990, 1994). Some species, such as the ferret, absolutely depend on prairie dogs, and others, including many reptiles and amphibians, are strongly associated with prairie dog towns. Twelve amphibian and 17 reptile species have been recorded from black-tailed prairie dog (*C. ludovicianus*) towns, and the lists do not appear to be exhaustive (Reading et al. 1989, Sharps and Uresk 1990). Where rocky outcrops are not available, prairie dog burrows may provide the only winter retreats for western rattlesnakes (*Crotalus viridis*) in northern sections of the Great Plains (Klauber 1972). Other reptiles and amphibians probably use prairie dog burrows as both summer and winter refuges and for nesting. Although no studies have been done, the elimination of prairie dogs may cause the local extinction of dependent segments of the herpetofauna.

Off-road vehicles

The effects of off-road vehicles are becoming an increasing concern in many grassland habitats, especially in drier areas that are near large population centers (Bury et al. 1977, Webb and Wilshire 1983). Busack and Bury (1974), Vollmer et al. (1976), and Bury et al. (1977) documented mild to drastic reductions in the species numbers and abundance of reptiles on Mojave Desert plots subjected to various degrees of off-road vehicle use. Severe off-road vehicle damage to arid grasslands is largely irreversible in any reasonable time frame, and unless managers can devise more effective ways of dealing with the problem, the rate of destruction will accelerate.

CONSERVATION CONCERNS

With few exceptions, the reptile and amphibian species associated with North American grasslands are widespread, common, and resilient, and they adapt to most perturbations, short of urbanization or crop farming. In the past, the large-scale conversion of grasslands to cropland has been the most damaging force, but no species have been lost on a global scale. Now that the grassland conversion process is mostly complete, the greatest danger to the herpetofauna is the cumulative effect of many small perturbations. Some of these (e.g., highway construction, urbanization, off-road vehicles, campground development) are almost always destructive, but others (e.g., check dams on small streams, irrigation schemes, land drainage, brush and tree invasion) may favor some elements of the herpetofauna, usually at the expense of other segments. These numerous, small-scale disturbances are difficult to monitor. An even more difficult challenge will be convincing management agencies that these perturbations need to be evaluated to see if they should be minimized or eliminated (Parmenter et al. 1994). In the aggregate, however, these habitat losses can spell the doom of a local fragment of a once cohesive herpetofauna.

The widespread continuing degradation of grasslands used as rangelands is a seemingly intractable problem. Many native grassland types are in danger of extinction by replacement with exotic stands. Management should focus on maintaining patches of sufficient size to provide refugia for lizards, such as *Cnemidophorus inornatus*, *C. uniparens*, and *C. neomexicanus*, that are thought to be dependent on these native plant formations. We need detailed information on the implications to the herpetofauna of changing the structure and species composition of grasslands by exotics like buffleggrass and Lehmann's lovegrass (W.G. Whitford personal communication).

Most of the species in the grassland herpetofauna are still widespread and secure; however, there are several areas that harbor relict species with very restricted ranges such as the dune lizard, the reticulate collared lizard, and the spot-tailed earless lizard described above (table 4). Many states protect species that barely enter their borders (e.g., species of the "Prairie Peninsula" of

Table 4. Areas of North American grasslands that support threatened species, subspecies, and populations of reptiles and amphibians.

Area	Species	Current threats
Mexican plateau	Bolson tortoise <i>Gopherus flavomarginatus</i>	Human predation ¹
South Texas, northeastern México	Reticulate collared lizard <i>Crotaphytus reticulatus</i> Spot-tailed earless lizard <i>Holbrookia lacerata</i> Black-spotted newt <i>Notophthalmus meridionalis</i>	Invasion of exotic grass, agriculture ²
Laramie Basin, Wyoming	Wyoming toad <i>Bufo hemiophrys baxteri</i>	Agriculture, unknown causes ³
Southeastern New Mexico, western Texas	Dune lizard <i>Sceloporus arenicolus</i>	Oak control ⁴
Illinois, Iowa, Missouri	Yellow mud turtle <i>Kinosternon flavescens</i> (northeastern populations)	Habitat loss ⁵

¹ Morafka 1982

² A.H. Price (personal communication)

³ Corn 1994

⁴ H.L. Snell (personal communication)

⁵ Dodd 1983

Illinois), but the only forms that appear to be genuinely threatened with extinction are the few relicts with restricted distributions resulting from post-Pleistocene climatic changes.

The Bolson tortoise (*Gopherus flavomarginatus*) of the Mexican plateau is a grassland species with special problems (Morafka 1982). Human predation for food, exacerbated by recent colonization of large ranches of northern Mexico, has reduced the tortoise to small scattered enclaves. Fortunately, efforts to protect the tortoise on an 18,000 ha private ranch in northern Mexico have apparently been successful, and it is hoped that the same sort of agreement can be obtained from other ranches that harbor tortoises (Anonymous 1994). Measures agreed to by the ranch's owners include modification of grazing rotations to protect hatchling tortoises and hiring of a part-time warden to patrol for poachers.

Habitat destruction and possibly pesticide use is responsible for the endangerment of other grassland species with limited ranges. The black-spotted newt (*Notophthalmus meridionalis*) of the lower Rio Grande (Río Bravo) Valley of Texas and

Mexico is an imperiled grassland species. Agriculture has destroyed many of the temporary ponds used by newts in the valley floor, but it still may be fairly common on large cattle ranches that are inaccessible for biological surveys (A.H. Price personal communication). The Wyoming toad (*Bufo hemiophrys baxteri*) did not breed in the wild from 1992-1994, but some adults were still present in 1994 (Corn 1994 personal communication). Pesticide use has been suggested as a reason for their demise, but evidence is lacking. Northeastern relict populations of the yellow mud turtle (*Kinosternon flavescens*) in Illinois and Iowa have been reduced to a few widely scattered ponds because of habitat destruction (Dodd 1983).

In the grasslands of the northern United States and southern Canada (Alberta, Colorado, the Dakotas, Iowa, Saskatchewan, Utah, Wyoming), there is a conservation issue of special concern. Western rattlesnakes, bullsnakes, racers (*Coluber constrictor*, *Masticophis taeniatus*), common garter snakes (*Thamnophis sirtalis*), and a few other snakes congregate in large numbers at widely scattered den sites in rocky outcrops or prairie dog towns

(Woodbury 1951). Here they are susceptible to decimation by killing, commercial exploitation, and prairie dog control efforts. Anecdotes of killing hundreds and even thousands of rattlesnakes in one year at a single den site were common in the past (Klauber 1972). There is no indication that any of these species are especially endangered, but their denning needs make them vulnerable to future overexploitation or decimation.

MANAGEMENT CONSIDERATIONS

Many species depend on either temporary or permanent bodies of water, and most forms that have suffered declines are associated with water or riparian vegetation. For this reason, water provision will often have the greatest immediate effect on local herpetofaunal species richness, especially on drier western and southwestern ranges.

Intensive grazing, grass plantings, brush removal, prairie dog control, off-road vehicle use, and other activities that reduce habitat complexity usually decrease the number of species of reptiles and amphibians. Management techniques that open up grasslands or encourage scattered trees and shrubs should have the most value in dense, well-watered eastern and northern areas. The greatest research needs are those directed at the effects of water provision, burning, grass planting, and overgrazing on various segments of the herpetofauna.

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Grassland bats and land management in the Southwest

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Abstract.—Of the bat research that has been conducted in the Southwestern states, few studies have addressed species inhabiting grasslands and the potential effects of management activities on these populations. Up to 17 bat species may be found regularly or occasionally in Southwestern grasslands or short-grass prairie. Main habitat requirements of grassland-dwelling bats are suitable roosts, water, and food. Livestock grazing, fire suppression, mining, bridge construction, agriculture, and urbanization affect the quality, quantity, and distribution of these resources. Effects of activities may not always be negative. Management activities and the natural distribution of roost, water, and food resources ultimately influence the distribution, abundance, and species composition of bats in grasslands. Research is needed to further identify resource requirements and use by grassland-dwelling bats and to confirm specific effects of human activities on local populations.

INTRODUCTION

Among the many objectives of ecosystem management are the preservation of viable populations of species native to the ecosystem, and the protection and maintenance of ecological processes and species interrelationships (Grumbine 1994; Thomas 1994). Nonetheless, much of the information needed to achieve these objectives is unknown. In this paper, Southwestern grasslands refers to the plains-mesa and desert grasslands of New Mexico and Arizona (Lowe and Brown 1973; Dick-Peddie 1993; McClaran 1995). To balance human use and conservation of these arid grasslands, knowledge of the life history, habitat requirements, interrelationships of animals, and the effects of management practices on different species is necessary.

Bats, the only true volant mammals, are a most unique, but often overlooked, group of animals. Bats feed on nocturnal flying and terrestrial insects, and likely play a role in regulating insect populations (Ross 1967) and insect-related ecological processes. By helping to maintain a balance of relationships within the insect community, and

between insects and plants, animals, and other entities, bats are integral to the function and integrity of many ecosystems. The diverse habitats of New Mexico and Arizona support up to 28 species of bats (Findley et al. 1975; Hoffmeister 1986), many of which are found regularly or occasionally in grasslands.

This paper reviews the basic habitat requirements of bats, bat species that use grassland habitats, and the potential effects of historic and current management practices on resources important to grassland-dwelling bats. The information in this review will provide land managers with a better understanding of bats and the potential influence of human activities on bats in Southwestern grasslands.

HABITAT REQUIREMENTS OF SOUTHWESTERN BATS

Appropriate roosts, available surface water, and food are essential components of suitable bat habitat in the Southwest. Because of their small size, the energetic demands of flight, a limited ability to store fat, and the seasonal abundance of their prey, bats have an annual energy budget that is difficult to balance (McNab 1982). Energy expen-

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ditures are regulated through roost selection (Kunz 1982; Hill and Smith 1984). Consequently, reproductive success and overwinter survival of individuals and populations may largely depend on the availability of suitable roosts (Humphrey 1975). For colonial bats, suitable maternity roosts provide a microclimate that facilitates gestation in pregnant females and rapid growth of the young (Humphrey 1975). Appropriate winter hibernacula (hibernation sites) minimize the potential for disturbance and arousal and maximize efficient use of energy reserves. Therefore, overall distribution and abundance of suitable roost sites (summer and winter) may ultimately determine the distribution and abundance of many bat species (Humphrey 1975). Local distribution and site use may also be influenced by factors unknown to or unstudied by the scientific community such as threat by predators, distance to or availability of local hibernacula, and sensitivity to human disturbance.

Surface water for drinking is another critical component to bat habitat in the Southwest. Due to their high protein diet, insectivorous bats require water to excrete toxic nitrogenous waste products (McNab 1982). In addition, desiccating environments cause high rates of evaporative water loss through wing membranes and respiratory exchange (McNab 1982). California myotis (*Myotis californicus*), western pipistrelle (*Pipistrellus hesperus*), pallid bat (*Antrozous pallidus*), and the Mexican free-tailed bat (*Tadarida brasillensis*) have high urine-concentrating abilities or renal structures that suggest they produce highly concentrated urine (Geluso 1978). As a result, these arid-dwelling bats are more efficient at conserving water. More mesic species with distributions that include or extend into grasslands and deserts (long-legged myotis [*Myotis volans*], fringed myotis [*M. thysanodes*], little brown myotis [*M. lucifugus*], Yuma myotis [*M. yumanensis*], Townsend's big-eared bat [*Plecotus townsendii*]) have low urine-concentrating abilities (Geluso 1978) and probably select habitat with a greater emphasis on water availability.

Based on physiological adaptations to water conservation or lack thereof, bats must find roosts and foraging areas that have water within an economical flight distance. Bats foraging in grasslands and desert scrub probably seek water at

stock- tanks, perennial streams, drainage ditches, or the closest river. Prior to livestock grazing, bats may have relied on sparsely distributed springs, seeps, and permanent water sources. Historically, the geographic distribution of species not adapted for water conservation or for long distance flight may have been limited by water availability. However, construction of water holes and placement of stock tanks in Southwestern grasslands over the last 100- 150 years have increased the quantity and distribution of water available. Areas originally devoid of water may have become viable roosting and foraging habitat to other bat species (Geluso 1978). Because few records document bat distributions prior to livestock grazing in the Southwest, it is impossible to confirm whether ranges of such species (e.g., fringed myotis, long-legged myotis, etc.) have expanded into grasslands and deserts due to the increased number of water holes and stock tanks.

Food availability also determines bat species distribution and habitat use. Although insects appear to be so abundant as to preclude competition between bat species (Ross 1967; Humphrey 1975), dietary partitioning among insectivorous bat species may be evident from their wide range of sizes, flight styles, echolocating abilities, and the partitioning of vertical and horizontal space during foraging (Black 1974). Nonetheless, our understanding of the food habits and dietary preferences of insectivorous bats is extremely limited. Nondestructive methods of studying diet, the difficulty with which arthropod remains are identified and quantified in feces, and the lack of methods to effectively sample species composition and seasonal abundance of arthropods have limited the number of dietary studies conducted. The insect orders *Lepidoptera* (moths) and *Coleoptera* (beetles) are numerous and diverse and probably represent a universally available food source for most bat species (Ross 1967). In New Mexico, California myotis, western pipistrelles, and long-legged myotis are classified as moth strategists, and pallid bats, long-eared myotis (*M. evotis*), and fringed myotis are classified as beetle strategists (Black 1974). However, all of these species consume a diversity of arthropods in addition to moths and beetles, including *Orthoptera* (grasshoppers), *Hymenoptera* (bees/wasps), *Diptera* (flies), *Homoptera* (leafhoppers), *Hemiptera* (true bugs),

and *Isoptera* (termites) (Ross 1967; Black 1974; Whitaker et al. 1981). Diet composition also likely reflects seasonal peaks of different arthropod species (Black 1974) and probably varies with habitat type. Consequently, differences in insect fauna between two habitat types may cause grassland-dwelling bats to have different diets than individuals of the same species from adjacent habitats. Further studies of insect availability and dietary preferences and requirements of bats are needed to interpret the effects of human activities on bat populations.

BATS OF SOUTHWESTERN GRASSLANDS

In the eastern half of New Mexico, plains-mesa grasslands grade into and, depending on the classification scheme, are considered part of the short-grass prairies of the Great Plains (Wright and Bailey 1980; Dick-Peddie 1993). Because these grassland types are similar and animals do not recognize artificial boundaries, bats found in Southwestern grasslands (New Mexico and Arizona) and short-grass prairie (northern Texas, western Oklahoma, southwestern Kansas, and

Table 1. Federal status and types of summer roosts used by bats in Southwestern grasslands and short-grass prairies.

Species	USFWS status	Types of summer roosts
Species more commonly associated with grasslands		
Small-footed myotis (<i>Myotis ciliolabrum</i>)	Species of concern	Cracks and crevices of cliffs and rocks, abandoned buildings and barns, under rock slabs and loose bark; possibly in caves and mine tunnels.
California myotis (<i>M. californicus</i>)		Cliffs, hillsides, rock outcrops, mine shafts, barns, houses, under tree bark and sign boards, amongst desert shrubs, and on the ground.
Cave myotis (<i>M. velifer</i>)	Species of concern	Primarily caves and tunnels; occasionally buildings, bridges, and under rocks.
Pallid bat (<i>Antrozous pallidus</i>)		Rocky outcrops, crevices, caves, mine tunnels, buildings, and under rocks.
Western pipistrelle (<i>Pipistrellus hesperus</i>)		Canyon walls, cliffs, and other rock crevices; under rocks, in burrows and buildings.
Mexican free-tailed bat (<i>Tadarida brasiliensis</i>)		Caves, mines, bridges; occasionally in buildings.
Species found in grasslands given appropriate habitat		
Little brown bat (<i>M. lucifugus</i>)		Buildings, hollow trees, natural crevices, mines.
Yuma myotis (<i>M. yumanensis</i>)	Species of concern	Crevices, mines, caves, buildings.
Fringed myotis (<i>M. thysanodes</i>)	Species of concern	Caves, mine tunnels, rock crevices, old buildings.
Long-legged myotis (<i>M. volans</i>)	Species of concern	Abandoned buildings, cracks in ground, cliff face and other crevices, under loose bark.
Long-eared myotis (<i>M. evotis</i>)	Species of concern	Tree hollows, loose bark, folds of wood/bark, rock crevices, abandoned buildings, mines.
Hoary bat (<i>Lasiurus cinereus</i>)		Foliage of trees and shrubs.
Silver-haired bat (<i>Lasionycteris noctivagans</i>)		Hollow trees, woodpecker holes, under loose bark, and in buildings.
Eastern red bat (<i>Lasiurus borealis</i>)		Foliage of trees and shrubs, clumps of Spanish moss.
Big brown bat (<i>Eptesicus fuscus</i>)		Hollow trees, rock crevices, mine tunnels, caves, buildings; occasionally in cliff swallow nests.
Townsend's big-eared bat (<i>Plecotus townsendii</i>)	Species of concern	Caves, mine tunnels, and abandoned buildings.
Spotted bat (<i>Euderma maculatum</i>)	Species of concern	Cracks and crevices in rocky cliffs or under loose rocks.
Big free-tailed bat (<i>Nyctinomops macrotis</i>)	Species of concern	Crevices in rocky cliffs, buildings.

eastern Colorado) have been reviewed together. Information in this paper has been drawn from state mammal fauna texts (Findley et al. 1975; Bee et al. 1981; Hoffmeister 1986; Schmidly 1991; Armstrong et al. 1994), related literature, and personal observation. The United States Fish and Wildlife Service classification for the species and types of structures used as summer roosts are in table 1.

The structure and complexity of vegetation and the physical environment are factors that determine the use of habitats by vertebrates (Humphrey 1975; Grant et al. 1982; Parmenter et al. 1994). The apparent lack of vertical structure in grasslands seemingly indicates a lack of roosts and roost diversity for bats. However, animal size and mobility determines the scale at which habitat selection occurs. A high degree of mobility allows bats to select habitats at the landscape level and to utilize patches of resources that are separated by significant distances (Kunz 1982; Schmidly 1991). Their small size allows them to exploit practically any sheltered site. Most grasslands encompass patches of other habitat types (Parmenter et al. 1994) and thus provide a surprising diversity and abundance of roost sites. Bat roosts within grasslands may include crevices in and under stones and rocks, excavated or natural holes in the ground, and the foliage of scattered shrubs and trees. Interspersed within grasslands, patches of other habitat types such as rock escarpments, talus slopes, cliff faces, lava flows and tubes, caves, open mines, and bridges, provide a host of different roost environments for grassland bats. In addition, bats may roost within the foliage, bark, and cavities of riparian vegetation along arroyos, tributaries, and rivers that pass through grasslands.

Bat species commonly captured within Southwestern grasslands and short-grass prairies are the more xeric-adapted bats, including small-footed myotis (*Myotis ciliolabrum*), California myotis, western pipistrelle, pallid bat, cave myotis (*M. velifer*), and the Mexican free-tailed bat. Small-footed myotis are grassland-adapted bats that often roost in rocky outcrops found throughout short-grass prairies (Bogan In press). This species is documented from chalk bluffs and canyons in western Kansas and the grasslands of eastern Colorado (Robbins et al. 1977, Armstrong et al. 1994). Twenty-four percent of the small-footed myotis museum specimens in the Museum for

Southwestern Biology were collected from grasslands or riparian habitats within grasslands (Findley et al. 1975).

Occurring from deserts to ponderosa pine forests, California myotis is one of the more common species captured in grasslands (O'Farrell and Bradley 1970; Findley et al. 1975). Aside from nursery colonies, which may roost communally in one location most of the summer, small groups and individual California myotis show little roost site fidelity. California myotis appear to have flexible roosting habits and a ubiquitous supply of roosts; thus, they have little loyalty to any one site (Krutzsch 1954; Hirschfield et al. 1977).

Western pipistrelles occur from desert scrub to ponderosa pine forests, but are most commonly found near rocky cliffs and canyons in desert and grassland environments (Findley et al. 1975; Hoffmeister 1986). Although pipistrelles typically roost in canyon walls, rocky cliffs and outcrops, and under rocks on the ground, they are also found dayroosting in mine shafts and buildings.

A common inhabitant of Southwestern deserts and grasslands, the pallid bat is frequently found around rock outcrops and water, but also in areas devoid of these features (O'Farrell and Bradley 1970; Findley et al. 1975). Roosting in rock crevices and man-made structures, males and female pallid bats are gregarious with members of the same sex (Hermanson and O'Shea 1983).

Another desert and grassland bat, the cave myotis, is found in the grasslands of Texas, western Oklahoma, southcentral to southwest Kansas, and southern New Mexico and Arizona (Kunz 1974; Findley et al. 1975; Bee et al. 1981; Caire et al. 1984; Hoffmeister 1986; Schmidly 1991). The cave myotis roosts colonially in caves and mines and is often found foraging over watercourses in deserts and grasslands (Hayward 1970; Findley et al. 1975; Fitch et al. 1981).

Mexican free-tailed bats are common in pinyon-juniper woodlands, desert grasslands, and desert. This species typically roosts colonially in caves, rock crevices, under bridges, or in buildings (Findley et al. 1975; Wilkins 1989). Adapted for fast and long distance flight, these bats are known to travel up to 50 miles to forage in a single night (Hoffmeister 1986).

Other features within grasslands provide additional types of roosting and foraging habitat and

allow many nonxeric-adapted bat species to occupy grasslands. Trees along streams and rivers provide roosts to hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), and eastern red bats (*Lasiurus borealis*) (Findley et al. 1975; Hoffmeister 1986; Armstrong et al. 1994). Watercourses, trees, and man-made structures also provide foraging and roosting habitat for broadly distributed species such as big brown bats (*Eptesicus fuscus*), little brown bats (*M. lucifugus*), and Yuma myotis (Jones 1965; Findley et al. 1975; Barclay and Cash 1985; Hoffmeister 1986; Armstrong et al. 1994). Scattered caves, mines, buildings, and lava tubes found throughout grasslands provide roosts for Townsend's big-eared bats and big free-tail bats (*Nyctinomops macrotis*) (Findley et al. 1975, Humphrey and Kunz 1976; Kunz and Martin 1982; Caire et al. 1984; Genter 1986; Hoffmeister 1986). A Townsend's big-eared bat and Yuma myotis captured over an isolated desert spring in Nevada indicate that these species may venture into desert areas practically devoid of water (O'Farrell and Bradley 1970). Rocky cliffs and canyons may provide summer roosts for spotted bats (*Euderma maculatum*) (Findley et al. 1975; Schmidly 1991). Originally thought to occur primarily in mesic areas like ponderosa pine and mixed conifer, spotted bats have also been found in xeric habitats of Utah (Geluso 1978; Storz 1995). The ability of spotted bats to concentrate their urine indicates that this species may have evolved in more arid environments such as deserts and grasslands (Geluso 1978).

Species with centers of distribution in other habitat types that may occur peripherally in grasslands include the fringed myotis and long-legged myotis. Although long-legged myotis and fringed myotis typically occur in pinyon-juniper, oak woodland and higher elevations, they have been occasionally captured in grasslands and desert in New Mexico and Arizona (O'Farrell and Bradley 1970; Findley et al. 1975; Hoffmeister 1986). A maternity colony of fringed myotis near Isleta Cave in New Mexico likely foraged in nearby grasslands (Findley et al. 1975). In Texas, the long-legged myotis is rare, but fringed myotis are present and seem to prefer grasslands at intermediate elevations (Schmidly 1991). In pinyon-juniper woodlands of New Mexico, long-eared myotis frequently nested in folded bark and wood of

junipers, tree stumps, and small groups of rocks (pers. obs.). Thus long-eared myotis may be found using these structures where available in grasslands.

Information on habitat distribution and roost selection by different bat species comes from netting records, museum specimens, and observations. However, records are not complete throughout each species' geographic range, not all habitat types have been sampled equitably, and all sampling techniques are somewhat biased. Thus, sampling techniques used and areas and habitats sampled should always be considered when evaluating the geographic presence or absence, habitat associations, and habitat requirements of different bat species. Southwestern grasslands and short-grass prairies probably have not been sampled as extensively and thoroughly as other habitat types. Additional studies (e.g., surveys, radiotelemetry, light tagging, etc.) in grassland areas would contribute to a comprehensive understanding of which bat species use grasslands and which habitat components are important.

EFFECTS OF CURRENT AND HISTORIC MANAGEMENT PRACTICES

The quantity, quality, and distribution of resources available to bats in grassland environments have been altered by historic and current management practices. Activities that have probably had major influences on roost, water, and foraging resources of bats in grassland areas include grazing, fire suppression, mining, road and bridge construction, agriculture, and urbanization. Human activities often change the structure, composition, and distribution of vegetation and other resources at a local or landscape level. Because of different resource requirements, some wildlife species benefit from human-induced changes and some experience negative impacts. Grazing outside a cattle exclosure resulted in a shift to bird and small mammal species that preferred more xeric and open habitats. Inside the exclosure, species preferring mesic and densely vegetated habitats remained (Bock et al. 1984). Grassland fires adversely affect wildlife species that prefer dense litter and woody plant cover, but enhance habitat for species that prefer large-seeded herbaceous dicots (MacPherson 1995).

Little research has been conducted to determine how human activities may change landscapes to benefit or adversely affect different bat species in Southwestern grasslands. The effects of grazing, fire suppression, urbanization, etc. can only be speculated based on the effects of these activities on known resource requirements of bats.

The distribution and availability of water to grassland bats have largely been influenced by livestock management practices and to some degree by urbanization. In addition to altering plant species composition and abundance in riparian areas, livestock can also eliminate riparian areas through channel widening, channel aggradation, or lowering of the water table (Saab et al. 1995). The impacts of cattle on Southwestern grasslands for over 100 years has likely led to the degradation or elimination of many native water sources (seeps and springs). However, numerous steel and dirt stock tanks created throughout grasslands and other arid habitats have increased the quantity and distribution of water to bats. Thus, populations of native grassland and desert-adapted bat species may have actually benefited from this grazing practice. In addition, less xeric-adapted bat species from adjacent pinyon-juniper, oak woodland, and riparian habitats may have expanded their distributions into grassland areas that were previously unsuitable. However, individuals of these species cannot rely on these man-made water sources. Tank pumps are turned on and off depending on the presence or absence of cattle at particular sites, and the fill status of many dirt stock tanks is dependent on seasonal precipitation. The growth of cities in or bordering on grasslands has also affected the availability of water to grassland-using bats. Pools, ponds, irrigation and drainage ditches, and other accumulations provide water to bats willing to colonize urban areas (e.g., big brown and little brown bats).

The two other essential resources to bats, roosts and food, are either directly or indirectly affected by human activities. The direct influence of stock tanks, mines, and man-made structures on bat roosting behavior, habitat use, and species distribution is evident by their use of these structures. This influence is somewhat quantifiable through capture, mine surveys, and examinations of bridges, buildings, and other structures. However, the effects of other human activities such as graz-

ing, fire suppression, and agriculture are indirect, complex in nature, and not readily apparent. Such effects are difficult to assess and remain unstudied.

Abandoned underground and surface mines in New Mexico have significantly increased the number of potential sites for day and night roosts, maternity colonies, hibernacula, and migratory stopovers for bats. Twenty-nine of the 42 species in the United States use abandoned mines to some degree (Belwood and Waugh 1991). Twenty percent of mine features examined in New Mexico in one year showed enough bat use to warrant the gating of entrances instead of mine closure (Altenbach and Milford 1991). A minimum of 1800 underground mines and 3400 surface mines exist on or near national forests in New Mexico alone (Shields et al. 1995). Mining has created an enormous supply of potential roost sites to cave and rock-dwelling bat species and those that have been displaced from their traditional roosts. However, the closure of abandoned underground mines occupied by reproductive or hibernating bats has probably been the demise of many hundreds or thousands of bats. Bridges, houses, barns, and other man-made structures found throughout grasslands have also increased the number and type of roosts available to many bat species. However, many modern structures are built to exclude bats, older buildings are often bat-proofed by their owners, and newer bridge designs may not be suitable for occupation by bats (Keeley and Bloschok 1995).

Human activities influence the food and roost resources available to bats indirectly by altering the structure and composition of vegetation at local and landscape levels. Grazing and fire suppression interact to influence the number and types of roosts available to bats and perhaps more significantly, the species composition and abundance of their prey base. General consensus exists that historic grazing and a subsequent reduction in fire frequency has led to a decrease in grasslands and an increase in desert shrubland (Branson 1985; Dick-Peddie 1993; MacPherson 1995; Saab et al. 1995). By compacting soil, removing plant cover, and indirectly reducing water infiltration, cattle decrease vegetation density and alter plant community structure and composition (Saab et al. 1995). The reduction of fine fuels to support the spread of fire and fire suppression by humans are probable causes for the decrease in fire frequency

in the past 130 years (Wright 1980; MacPherson 1995). Without fire to suppress the recruitment and growth of woody plants and because of the collection of fertile, but loose interspace soils under shrub canopies, many grasslands have been converted to desert shrubland or juniper savanna (Schlesinger et al. 1990; Loftin et al. 1995; MacPherson 1995).

Although some bat species (e.g., California myotis) may benefit from the additional roosts provided by shrubs and other woody plants, the more significant impact on the local bat community may be the change of insect fauna from grassland species to desert shrubland or juniper savanna species. Studies in Parmenter et al. (1994) suggested that grazing and other rangeland disturbances favor pest grasshopper species. Although such changes may affect pallid bats that forage on such large terrestrial prey, the type of influence is unknown and depends on the degree of species-specificity in the pallid bat's diet, the availability of alternative prey, differences in prey behavior, nutritional value, predator defenses, and other factors. The effects of fire on various arthropod species are reviewed in Warren et al. (1987). However, fire suppression, not prescribed fire, is the more prevalent management activity today and the consequence of historic management practices. Considering that more than 1200 insect species from 11 orders feed on grasses in Arizona, New Mexico, Utah, Nevada, and Colorado (Warren et al. 1987), there is an insufficient number of studies to provide a comprehensive overview of the effects of grazing and fire suppression on arthropod community composition, structure, and distribution. In addition, too little is known about diet and prey selection by grassland-dwelling bats to predict their responses to changes in the arthropod community. Knowledge of these factors would be useful for interpreting the effects of agriculture, including the cultivation of monoculture crops and the application of pesticides, on the prey base of bats.

The diversity of arthropod orders found in guano of any one bat species suggests a degree of dietary plasticity in bats. However, differences in size, flight style, and echolocating ability may restrict each bat species to a certain prey size range (Ross 1967). Perhaps as long as certain prey community characteristics (e.g., insect size distribution,

activity patterns, seasonal peaks of abundance, etc.) are consistent, changes in insect species composition may not greatly affect bats that have flexible diet preferences. Bats in grasslands may be resilient to changes in insect fauna caused by human activities and even opportunistic of insects associated with agricultural fields, irrigation ditches, street lamps, and other man-made structures, but such speculations should be demonstrated, not assumed.

RESEARCH IMPLICATIONS

An increasing number of land managers are concerned with conserving bats, protecting critical bat habitat, and maintaining the role of bats in ecosystem processes. Perception of bats by the public is improving as conservation educators focus on the value of bats and dispel myths and negative images. Most importantly, more scientists are reducing the deficit of information on the life history, habitat requirements, community structure, and roles of bats in ecosystems. Much of what is known about bats originates from research focused on bats in forested environments, caves, and manmade structures. The lack of information on grassland-dwelling bats and the potential effects of management activities is apparent from this review. Information from studies examining the resource requirements of grassland-dwelling bats may subsequently be used to predict the potential effects of human activities on bats or to design studies that measure actual effects. Recommendations for future research include:

- Develop a comprehensive understanding of composition, distribution, and abundance of bats in grasslands. Conduct mist net, acoustical, and cave and mine surveys at previously unsurveyed sites to provide a thorough coverage of grassland habitats.
- Determine what landscape features are used by bats in grasslands and for what purposes. Use radiotelemetry and light tagging to observe bat behavior, follow movements, and identify day and night roost sites. Knowledge of which features are used by bats and seasons of use will allow planning of activities to minimize impacts on local bat populations.

- Identify food habits of grassland bats so that dietary flexibility may be determined and the effects of management activities may be predicted. Determine foraging areas, food availability, and diet preference by radiotelemetry, arthropod sampling, and fecal analyses, respectively. Basic studies of the effects of grazing, fire, etc. on arthropod communities are also necessary.
- Examine effects of human activities on bat communities. Compare bat species composition, abundance, and behavior before and after implementation of activities (prescribed fire, new grazing regime, etc.), or between treated and untreated sites.
- Determine if availability and diversity of water, roost, or food resources influence bat species diversity and abundance. Examine such correlations by coupling bat surveys with evaluations of resource availability and diversity in the surrounding area. Studies that manipulate water availability and monitor bat activity may also determine the effect of water availability on use of grasslands by bats in the arid Southwest.
- Investigate winter behavior and roost habits. Determine whether grassland bats migrate to hibernacula or remain locally. If bats remain local, identify structures used as hibernacula and develop recommendations for maintenance and protection of these structures.

Our ability to understand bat ecology and management in grassland and other ecosystems increases as study techniques, technology, and interest by the research community develop. Using this information, managers may make more effective decisions regarding bat habitat, and educators may increase interest and appreciation for bats, their unique ecology and behavior, and their role in ecosystem function.

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Sparrow migration along a river corridor in desert grassland

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Abstract.—We analyzed trends of sparrows and towhees captured in fall at the Rio Grande Nature Center, Albuquerque, New Mexico from 1985 to 1994. Species were grouped into three breeding-habitat classes: grassland and shrubsteppe, riparian and deciduous vegetation, and upland forests, woodlands, and edges. Spearman's rank correlations were used to determine whether population trends were similar within and among species groups. We found that steep fluctuations in captures of many species masked population increases or decreases over time. Eight of nineteen (42%) correlations of pairs of species were significant within habitat groups. This indicated that some species populations fluctuated in similar ways, suggesting that shared factors on the breeding grounds may have influenced numbers captured in migration.

INTRODUCTION

The scarcity of water, food, and shelter in combination with the dry heat of semi-arid and arid grasslands and deserts in the western United States can pose formidable barriers to travel by animals adapted to living in moister, more vegetated environments. Many migratory songbirds use river corridors as flyways through arid grasslands because rivers supply suitable species-specific resources that may be lacking in the surrounding landscape (Finch et al. 1995). In this paper, we examined migration patterns of selected emberizid species using the Rio Grande in central New Mexico. The Rio Grande is an important flyway and wintering grounds for migratory geese and sandhill cranes (*Grus canadensis*), but less is known about its value to migrating songbirds (Yong and Finch 1996; Finch and Yong in press). In particular, our paper documents use of a western riparian corridor by sparrow species that breed in short-grass prairie and shrubsteppe of the Great Plains and interior West.

From Cochiti Dam to Elephant Butte, New Mexico, the floodplain vegetation of the Rio Grande is composed of deciduous riparian forest surrounded by desert grassland and shrubland (Finch et al. 1995; Whitney 1996). Although the riparian forest, locally referred to as the "bosque," has changed greatly since European settlement, it continues to be identified as one of the most important reservoirs for biological diversity in New Mexico (Finch and Yong in press). State and international conservation programs have recently been mobilized to protect the bosque's biological resources from threats such as water development, urban growth, exotic woody plant invasion, livestock grazing, arson, and recreational overuse (Whitney 1996). In this paper, we describe breeding and wintering distributions and fall capture trends of 12 migratory emberizid species (sparrows and towhees) along the middle Rio Grande over a ten-year period. Breeding habitats occupied by these migratory sparrows ranged from prairie grasslands and sagebrush to shrub thickets, deciduous riparian woods, and forest clearings and edges. We arranged species based on general similarities in use of breeding habitats and searched for patterns of population changes associated with specific species groups. We focused on

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emberizid species that breed in grasslands in particular because many of these species are reported to have declining populations (Finch 1991, Askins 1993, DeSante and George 1994, Herkert 1995).

METHODS

The Rio Grande Nature Center (RGNC) is located along the middle Rio Grande, Bernalillo County, New Mexico (35°07'N, 106°41'W). Rio Grande Bird Research, Inc., established a long-term banding station at RGNC and has mist-netted landbirds during fall migration since 1979. We used data collected from 1985 to 1994 because the netting effort was less constant during the first six years of the banding study. The study area was established in riparian habitat, and the sampling sites included woods, two human-made ponds, and agricultural fields. The banding location was excluded from public access, and habitat disturbance or modification during the study was not evident (Cox 1994).

Twenty mist nests (12m x 2.6m with 30 mm or 36 mm mesh) were used to capture and recapture landbirds from early August through mid-November each year. Nets remained at the same locations through the study period and were operated by volunteers during weekends in fall. Nets were opened about 15 minutes before local sunrise, were checked every 20-30 minutes, and remained up for approximately six hours each banding day. Nets were closed during rain, snowfall, and other excessive weather conditions (i.e., temperature > 38°C or winds > 40 km/h). Species, age, and sex identification were based on the North American Bird Banding Manual (U.S. Fish and Wildlife Service and Canadian Wildlife Service, 1984), Identification Guide to North American Passerines (Pyle et al. 1987) and various field guides. Each bird was banded with a U.S. Fish and Wildlife Service aluminum leg band (see Yong et al. 1995).

We treated yearly weekend mist-netting efforts as temporally stratified repeated samples. We recognized that daily capture totals of each species could be affected by factors such as weather conditions and species-specific seasonal migration patterns but considered these factors to be of stochastic influence on the annual totals and

population trends through the ten-year period. We adjusted the net hour variation among years by calculating yearly indices for each species by dividing the total number of captured individuals by the total number of net hours of a given year, and then multiplying the resulting numbers by 100. This produced a yearly estimate of birds/100 net hours of banding operation.

To evaluate patterns of migration within a taxonomic group, we focused on emberizids because (1) species diversity was high enough to detect patterns within this taxon, if patterns existed, (2) species differed in habitat use enough to detect trend differences between groups, if there were differences, and (3) several of the emberizid species caught in this study occupied western grasslands during the breeding season, and therefore, they were deemed appropriate subjects for addressing the grassland theme of this proceedings.

To examine population trends of emberizids captured at RGNC, we performed Spearman's rank correlation with year as one variable and birds captured/100 net-hours of each species as the second variable. We applied Spearman's rank correlation because captures were not normally distributed through time for some species (Zar 1984). Only common species with total capture numbers > 80 were used for population trend analyses. We defined trends as significant at $P < 0.1$. We chose this alpha level to reduce Type II error and increase chances of detecting population declines of migratory birds. If population problems can be detected early due to initial warnings from trend data, the species has a greater chance of population recovery through close monitoring and prompt conservation actions.

We also evaluated population trend data obtained from the Breeding Bird Survey (BBS), a large-scale program for monitoring numbers of North American birds coordinated by the National Biological Service (NBS) (U.S. Fish and Wildlife Service prior to NBS separation) and the Canadian Wildlife Service since 1966. BBS is a roadside survey, primarily encompassing the continental United States and southern Canada. The survey is conducted once a year during the peak of the breeding season. Each survey route is 39.4 km long with 50 stops at 0.8 km intervals along secondary roads. Observers start 0.5 hr before local sunrise

and at each stop count all birds detected within 0.4 km radius during a 3 min period (see Robbins et al. 1986).

We retrieved Breeding Bird Survey trend data for New Mexico, western United States, and continental United States from the NBS's database through the INTERNET. These trends were estimated using the route-regression method (Geissler and Sauer 1990). Regional trends were estimated as a weighted average of trends on individual routes. Route trends were estimated using the estimating equations estimator (Link and Sauer 1994) which calculates a multiplicative trend. Observer effects were incorporated into the model to prevent bias associated with increases in observer quality over time (Sauer et al. 1994).

To graphically illustrate possible patterns within and among groups of species, we grouped ten-year trends based on species use of breeding habitats: (1) prairies and grassland/shrubsteppe, (2) coniferous and mixed forests, clearings, and edges, and (3) deciduous woods, riparian thickets, and wet meadows. We treated Chipping Sparrow individually because its high abundance dwarfed the

trends of other emberizid species. To determine whether species with significant trend similarities clustered together, Spearman's rank correlation coefficients and alpha levels were arranged into a species-by-species display matrix.

RESULTS AND DISCUSSION

Twelve sparrow species with total samples greater than 80 captures from 1985 to 1994 were compared. Chipping Sparrow, White-crowned Sparrow, and Dark-eyed Junco were the most commonly-captured sparrow species, with Chipping Sparrow about four times more abundant than the White-crowned Sparrow or junco (table 1). Chipping Sparrows were more abundant than most other passerine species as well (Finch et al. 1995; Yong et al. 1995). Half of the 12 emberizid species bred primarily in Canada and the United States and wintered in Mexico and South America (fig. 1) and half had temperate breeding and wintering ranges that extensively overlapped (fig. 2). Green-tailed Towhees, and Brewer's, Lincoln's, and

Table 1. Breeding habitat and population trends of common migratory sparrows captured at Rio Grande Nature Center, Albuquerque, NM.

Common name	Scientific Name	Acronym ¹	BH ²	N	BT	NM	WE	US
Green-tailed Towhee	<i>Pipilo chlorurus</i>	GTTO	F	141	+		+	+
Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>	RSTO	R	126	-	+	+	-*
Chipping Sparrow	<i>Spizella passerina</i>	CHSP	F	4221	+	-	-	+
Clay-colored Sparrow	<i>Spizella pallida</i>	CCSP	G	86	+		-	+
Brewer's Sparrow	<i>Spizella breweri</i>	BRSP	G	202	-		-*	-*
Vesper Sparrow	<i>Pooecetes gramineus</i>	VESP	G	110	+	-	+	-
Lark Sparrow	<i>Chondestes grammacus</i>	LASP	G	426	+	-	-	-
Savannah Sparrow	<i>Passerculus sandwichensis</i>	SAVS	G	109	-		+	-
Song Sparrow	<i>Melospiza melodia</i>	SOSP	R	261	+		-*	+
Lincoln's Sparrow	<i>Melospiza lincolnii</i>	LISP	R	284	+		+	+
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	WCSP	R	1089	+		+	-
Dark-eyed Junco	<i>Junco hyemalis</i>	DEJU	F	915	-		-*	-*

¹ Common names and scientific names are based on the A.O.U. Check-list of North American Birds (1983). Acronyms are from USFWS (1984).

² BH = major breeding habitats (F = coniferous and mixed forests and woodlands, G = prairie grassland and shrubsteppe, R = riparian thickets and deciduous woods). N = the number of birds captured at Rio Grande Nature Center from 1985 to 1994. BT = population trends (Spearman's rank correlation) from banding data. NM, WE, and US = population trends from BBS data from 1980 to 1994 in New Mexico, western United States, and entire United States, respectively.

* $P < 0.1$ for BT, and $P < 0.05$ for NM, WE, and US.

White-crowned Sparrows were primarily western breeders in the United States, although Lincoln's and White-crowned Sparrows spread further north and east into Canada and northwest into Alaska during breeding. Clay-colored Sparrow was the only captured sparrow species whose breeding range (northern Great Plains, northern Midwest, and central Canada) was markedly disjunct from its wintering grounds south of the United States/Mexico border. Other species tended to be more continental in distribution, with Savannah Sparrow, Song Sparrow, Dark-eyed Junco, and Chipping Sparrow breeding into Alaska and much of Canada, and Rufous-sided Towhee, Lark Sparrow,

and Vesper Sparrow breeding widely east and west within the United States.

Based on RGNC data from 1985 to 1994, only Clay-colored Sparrow, Lark Sparrow, and White-crowned Sparrow exhibited significant trends (table 1). The positive trend for Clay-colored Sparrow was consistent with BBS trends for the continental United States over the same period of time. White-crowned Sparrow and Lark Sparrow showed positive trends in our study also, but BBS data did not show any matching trends at broader levels. BBS trends for other species varied with respect to significance and direction of trends between the western United States and the conti-

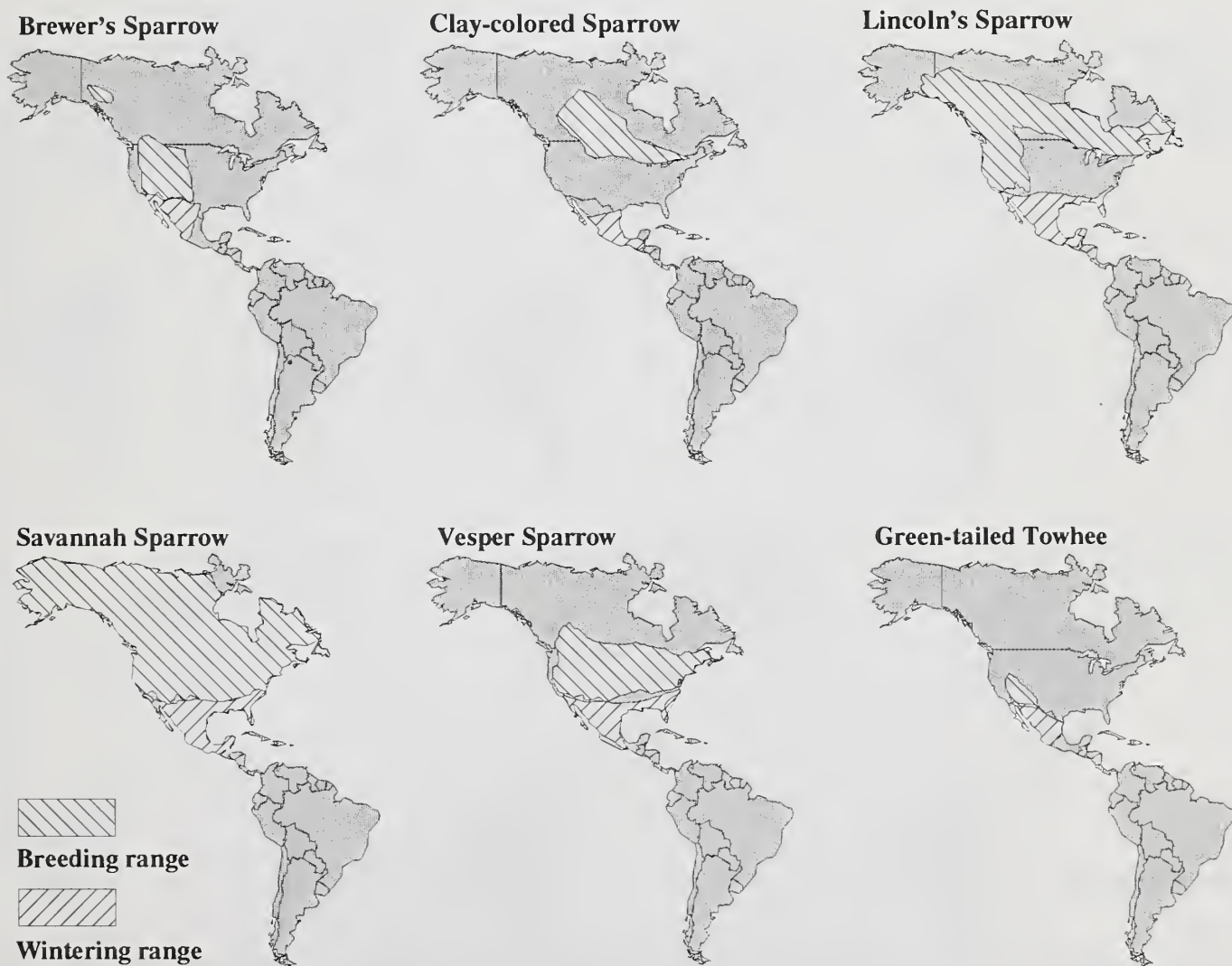


Figure 1. Distributions of six emberizid species commonly captured along the middle Rio Grande in fall that breed primarily in the United States and Canada and winter south of the U.S./Mexico border. Species names for each acronym are given in Table 1.

mental United States, except for Brewer's Sparrow and Dark-eyed Junco that showed significant declines at both levels. Except for four species that exhibited nonsignificant trends, BBS samples in New Mexico were generally insufficient for analysis. Patterns of population increases and decreases of species grouped by breeding habitat use or migratory distance were not evident based on RGNC or BBS data.

To further evaluate variation in numbers of RGNC-caught sparrows over the ten-year period, we classified species into habitat groups and graphed birds captured/100 net hours for multiple species/habitat. We defined Clay-colored,

Brewer's, Lark, Savannah, and Vesper's Sparrows as species that breed in prairie and shrubsteppe habitats; Rufous-sided Towhees, and Lincoln's, Song, and White-crowned Sparrows as species that breed in deciduous woods, riparian shrub, and wet meadow thickets; and Green-tailed Towhee, Dark-eyed Junco, and Chipping Sparrow as species that breed in coniferous and mixed forests and woodlands, especially along edges and clearings. Chipping Sparrow was graphed separately because its high abundance dwarfed numbers of other species, masking intraspecific variation. Patterns of population fluctuation among species were evident within and among habitat groups (fig. 3). Sharp



Figure 2. Distributions of six emberizid species commonly captured along the middle Rio Grande in fall that breed and winter primarily within the United States and Canada. Species names for each acronym are given in Table 1.

peaks and troughs in captures of many species canceled out increases and decreases over time, explaining why so few species trends were significant in our earlier trend analyses.

Thirteen (20% of 66) correlations of population trends in species pairs were significant, of which 8 of 19 (42%) were within habitat groups. All were positive suggesting that species tracked similar environmental conditions or resources and responded in a similar way when environments changed, rather than to avoid other sparrow species because of competition. Steep fluctuations, with a peak in 1989-90, a decline in 1991 and another peak in 1992, were conspicuous in the

three most common species, Chipping Sparrow, White-crowned Sparrow, Dark-eyed Junco, as well as in the most abundant grassland species, Lark Sparrow (fig. 3). Correlations of these four species were significantly positive for most pairs (table 2). The lack of a significant correlation between Chipping Sparrow and Dark-eyed Junco, however, is noteworthy because both species tend to use similar habitats and were initially grouped as such. Strong similarities in population trends among species that use a broad variety of habitats may be related to increased power to detect fluctuations owing to increased sample size; climate fluctuations such as periodic drought and precipitation

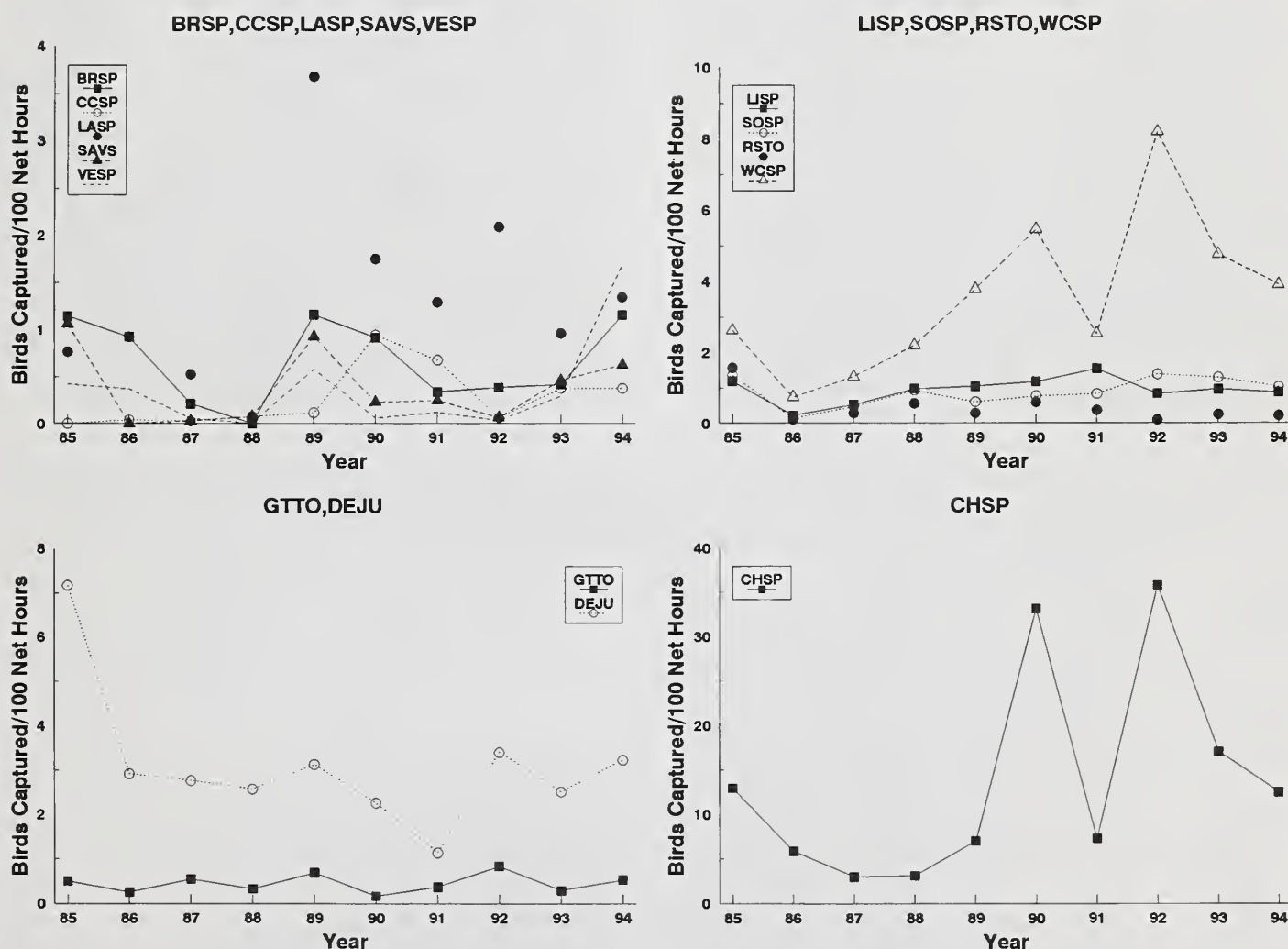


Figure 3. Numerical trends (captures/100 net hours) of 12 emberizid species caught from 1985 to 1994 at the Rio Grande Nature Center, Albuquerque, New Mexico. Species names for each acronym are given in Table 1. Species were grouped based on their breeding habitat use: grassland and shrubsteppe habitats (BRSP, CCSP, LASP, SAVS, VESP); deciduous and riparian habitats (LISP, SOSR, RSTO, WCSP); and coniferous and mixed forests and edges (GTTO, DEJU, CHSP). CHSP was graphed separately because of its high capture rates.

that cross vegetational boundaries; and changes in food supply related to climate.

Similarities in fluctuations within the grassland group included apparent declines by 1988 of all five species, peaks in 1989-90, declines by three species in 1992, and increases of all species by 1994. By arranging grassland species based on significant correlations (50% of 10 matches) among pairs, we confirmed that grassland species with similar trends clustered together (table 2), suggesting that similar factors caused populations of these species to covary over time. Factors that may induce species with sympatric distributions to vary in similar ways include changes in: weather and climate, food supply, availability of suitable habitat, predator densities, cowbird densities, pesticides, and disease rates. During a five-year study in Wisconsin and Michigan, Blake et al. (1989) also find that abundances of common species mostly varied in a parallel manner, indicating that they were influenced by the same or similar elements. They also found that annual variation in abundances of long-distance migrants was correlated with periodic drought. During a time of moderate to extreme drought (1986-1988), populations of more than 60% of the species, the majority being neotropical migrants, declined. They proposed that long-distance migrants may have been more

affected by drought than other species because they nested in June when effects of drought were most severe. Grassland sparrows in our study may be more susceptible to drought than riparian and forest sparrows because water is more limited in grasslands to begin with, such that a severe drought can decimate seed and insect food supplies. The declining trends of grassland species that we detected between 1985 and 1988 may have been caused by the same or similar drought conditions observed by Blake et al. (1989) during the same period.

While less obvious, numbers of riparian sparrows also significantly covaried in two pairs of species (Lincoln's Sparrow x Rufous-sided Towhee, and White-crowned Sparrow x Song Sparrow) over time (table 2). Capture rates of all four riparian species declined in 1986 and stabilized afterward except for WCSP (fig. 3). Numbers of Green-tailed Towhee and Dark-eyed Junco were also correlated, exhibiting a spatially isolated response in relation to other species pairs in table 1. Interestingly, DeSante and Geupel (1987) also reported a precipitous drop in captures in 1986 for many coastal breeding bird species in central California. This was related to significant reproductive failure associated with high rainfall during the breeding season. In general, reduced or increased productivity on

Table 2. Relationships between population trends of 12 sparrow species captured along the middle Rio Grande. Numbers represent Spearman's rank correlation coefficients (r), and symbols represent species pairs having significantly similar trends.¹ See table 1 for species names associated with each acronym.

Name	DEJU	GTTO	RSTO	LISP	SOSP	WCSP	CHSP	LASP	SAVS	BRSP	VESP
GTTO	0.61*										
RSTO	-0.26	-0.31									
LISP	-0.28	-0.15	0.81**								
SOSP	0.38	0.27	-0.01	0.25							
WCSP	0.12	0.16	-0.10	0.21	0.64*						
CHSP	0.14	-0.03	-0.07	0.26	0.69*	0.90***					
LASP	0.12	0.31	-0.27	0.15	0.12	0.71*	0.59*				
SAVS	0.25	0.18	0.45	0.67*	0.43	0.36	0.31	0.67*			
BRSP	0.50	0.10	-0.05	0.09	-0.02	0.25	0.26	0.54*	0.60*		
VESP	0.37	0.07	-0.06	0.12	0.25	0.02	0.05	0.32	0.65*	0.90**	
CCSP	0.50	0.10	-0.06	0.09	-0.02	0.25	0.26	0.51	0.21	0.04	0.06

¹ Analyses were based on birds captured/100 net-hours from 1985-1994. * $P \leq 0.10$; ** $P \leq 0.01$; *** $P \leq 0.001$.

the breeding grounds in any year should be reflected in capture trends of migrating hatching-year birds in fall. Therefore, reduced nesting success and low recruitment of young may explain the plunge in capture rates we observed for migrating riparian sparrows and the junco in fall 1986 and migrating grassland sparrows in 1987-88.

CONCLUSION

The middle Rio Grande valley supplies stopover habitat in fall for a variety of emberizid species that breed in prairie and shrubsteppe, riparian habitats, and deciduous and coniferous forests further north (Finch et al. 1995). Similar fluctuations in groups of species were detected using fall banding data, suggesting that populations of different species were similarly affected by factors common to either their breeding or wintering grounds. Given that fall trends reflect the numerical contributions of hatching-year birds, we deem it more likely that shared factors on the breeding grounds rather than on the wintering grounds were influential in determining capture numbers and species covariation in fall. While excessive rainfall or extreme drought could lead to the observed population fluctuations of some species in this study, other factors such as changes in available habitat structure and quantity, and effects of natural disturbances such as insect outbreaks, fire, and other climatic events are also important in interpreting population dynamics of migratory sparrows (Rotenberry et al. 1989). Avian population responses are dependent on species, habitat, and geography. To fully understand population trends of migratory birds, these variables need to be accounted for.

We did not detect consistent increasing or decreasing trends in groups of emberizid species. This is in contrast to studies that indicate populations of more species of North American grassland sparrows are declining than increasing in portions of their range (Askins 1993; Peterjohn et al. 1995). Our banding station is further west than the midwestern prairie states where species such as grasshopper sparrows (*Ammodramus savannarum*), dickcissels (*Spiza americana*), Henslow's sparrow, (*Ammodramus henslowii*), Brewer's sparrow, Clay-colored Sparrow, and Lark Sparrow are reported to have declined

over 1-3 decades (e.g., Central U.S. BBS, Peterjohn et al. 1995) and therefore, we may not have sampled migratory populations that nested in areas where apparent problems have been identified.

Riparian habitats are important to many more species than those that breed in them, including transients such as grassland and upland forest sparrows. Alteration and loss of riparian habitats throughout the Southwest (Rea 1983; Rosenberg et al. 1991; Ohmart 1994; Noss et al. 1995) may have potential to negatively affect migratory species that breed and winter elsewhere, by reducing the amount of suitable habitat they can stop at to find food and replenish fat stores (Finch and Yong in press). We recommend that greater efforts be focused on monitoring and conserving riparian habitats to ensure successful songbird migration. Unfortunately, information on what stopover habitats are important to transients is generally lacking in the western United States, so more research is also needed.

We also emphasize that songbird migration along interior western rivers cannot be fully interpreted without understanding the inseparable relationship of rivers to their arid and semi-arid surroundings. Likewise, to fully appreciate, sustain, and restore the physical and biotic resources and diversity of western grassland ecosystems, scientists, land managers, and conservationists must acknowledge and provide for the rivers and streams running through them.

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Integrating livestock production and wildlife in a sagebrush-grass ecosystem

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Abstract.—Management of a 775-km², privately-owned ranch in northeastern Utah exemplifies a progressive approach to utilizing domestic livestock and wild ungulates, elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*), for economic return while maintaining or enhancing land health. The management program on the Deseret Ranch includes the use of a multiple-herbivore grazing system in balance with the available forage and native wildlife in a sagebrush (*Artemisia* spp.)-grass ecosystem.

INTRODUCTION

The concept of supplementing domestic livestock production on private lands with economic utilization of wildlife is not new. Grazing systems based on multiple herbivore species can diversify revenue sources by buffering the effects of variable markets and forage production (Spedding 1988; Fleisher 1990; Riechers et al. 1989). In addition, multiple herbivore systems are thought to provide greater land health (Savory 1988; Heitschmidt and Stuth 1991) and prevent land degradation that jeopardizes long-term economic stability.

Examples of the integration of livestock production and revenues derived from recreational hunting on private rangelands include the Welder and McCan Ranch in Texas (Adams 1983), the Forbes Trinchera Ranch in Colorado (Freddy et al. 1991) and the Fort Apache Indian Reservation in Arizona (Jojola 1991). In this paper, we present a case history of how a large, private landholding (Deseret Ranch) can be managed for both profit and resource integrity. It should illustrate the potential synergism between profit, resource health, and people.

DESCRIPTION AND HISTORY OF THE RANCH

The Deseret Land and Livestock (DLL) property comprises 775 km² in northeastern Utah. The ranch has been privately owned since its formation in 1891. Historically, it was managed for sheep and wool production, at one time accommodating 60,000 ewes. During the second half of this century, emphasis shifted to cattle production. Elevations on the ranch range from 1,830 m to 2,740 m, with roughly equal areas of higher- and lower-elevation range. The former comprises largely montane meadows interspersed with conifer (*Pseudotsuga menziesii* and *Abies lasiocarpa*) and aspen (*Populus tremuloides*) stands, while sagebrush-grassland is the principal vegetation association on the latter. The ranch has a significant water share of the Bear River, providing the opportunity to irrigate approximately 8,000 acres. There are >150 km of riparian corridors. The elevational gradient and associated vegetational diversity, presence of riparian zones and a reservoir endow the Ranch with inherently high biological diversity. This diversity is augmented by results of past management practices. For example, substantial areas of lower-elevation sagebrush were treated by various means in the 1950's and 1960's. Some of these areas, planted to crested wheatgrass (*Agropyron desertorum*), have been reinvaded by

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sagebrush, producing a mosaic of horizontal and vertical structural diversity. As recognized by several investigators (Roth 1976; Wiens and Rotenberry 1981; Rothwell 1992), the resulting habitat heterogeneity attracts a diversity of grassland and shrub nesting birds.

During summer, the ranch currently supports 6,000 to 7,500 cattle and approximately 2,000 sheep. The ranch is ecologically well suited to the production of several wildlife species, especially native ungulates, and supports populations of approximately 3,500 mule deer, 2,200 elk, 100 moose (*Alces alces*), and 600 pronghorn. However, despite its large size, the ranch is only marginally suited to the production of large numbers of cattle due to limited availability of low-cost winter forage and the difficulty of effectively grazing the higher-elevation summer range without damaging riparian areas.

IMPETUS FOR CHANGE

Profit is essential for any private enterprise to survive. During the late 1970s, marginal profits from conventional livestock production prompted the ranch owners to consider economic alternatives for the property, including possible commercial and/or residential uses. This threat challenged ranch personnel to seek ways to generate profit while maintaining the land in a wildland state. They began with a careful evaluation of the production capabilities of the ranch. The four major land types on the property, namely irrigated lands, low-elevation crested wheatgrass areas, untreated sagebrush grassland, and higher-elevation mountain range, were examined to determine what "products" were best suited to each type, both economically and ecologically. The over-arching objective was that of managing ranch resources to provide year-round forage resources for both wild and domestic ungulates.

Following this assessment, a program to manage native ungulates for sustainable trophy hunting was implemented. This system featured careful management of age structure of the male segment of deer and elk populations with appropriate removals of antlerless animals to control population size.

Modifications of the cattle management program also were implemented to mimic the timing of parturition of large native ungulates such as bison (*Bison bison*) and elk. These included shifting the cattle breeding/calving cycle so the demands of lactation and breeding coincided with the peak of forage nutritional quality. Although calving now occurs 1-2 months later (early April) than previously (February), individual growth rates are higher with a lower cost per unit of weight. This shift reduced the reliance on baled winter hay by approximately half. Smaller-bodied cattle, which produced faster-growing calves, were selected as replacement heifers. Larger calves prevented cows from recovering sufficiently from lactation demands to breed each year in this low precipitation environment.

A grazing strategy was designed that mimicked the natural grazing patterns of large, herd-living ungulates. Cattle are grazed in one or two large herds, so that 90% of the cattle are grazing less than 10% of the land at any given time during the course of the growing season. During the period of rapid herbaceous growth of forage, cattle remain in a given "pasture" for less than a week.

These modifications resulted in decreased operating costs and increased profits, especially as a consequence of decreased reliance on hay to bring cattle through the winter months. The success of these innovative programs bolstered the confidence of ranch personnel and fostered an atmosphere conducive to trying other new ideas. The outcome was adoption of a mission statement that featured the concept of maximizing profit while maintaining or enhancing the integrity of the resource base.

MONITORING

A monitoring system was needed to determine whether mission objectives were being met. Ranch personnel felt they were effectively tracking profit, but the question remained as to what measures were appropriate to monitor resource health (i.e., condition and production capability). Several indices have been employed; among the simplest were plant condition and percent cover. The assumption was that decreasing the proportion of bare ground would increase water infiltration,

which was considered desirable. Other indices were plant species diversity (richness) and community structural heterogeneity, water flow and the condition of riparian vegetation as well as a year-round flow of clean water. A diversity of animal species (including insects) was considered desirable. Several measures of the condition of both wild and domestic ungulates have been monitored regularly. These include weight, production ratios, recruitment, and antler characteristics in relation to herd sizes and production goals. Through time, cost-effective methods of quantifying these “indicators” were devised and have been used both as indices and (in some cases) as predictive models.

PROGRESS AND OUTCOMES

The management changes described above have produced several positive responses. Based on data collected by the USDA Natural Resource Conservation Service (formerly Soil Conservation Service), percent plant ground cover increased by 6% during the period 1980-1986. The quality of riparian systems has been maintained or (in most cases) enhanced. Specifically, near-stream vegetation has increased and siltation has decreased, resulting in improved stream structure and increased perennial stream flow. Although as yet undocumented empirically, the improved plant structure in riparian habitats might be expected to result in a richer avifauna (Bock et al. 1984; Knopf et al. 1988).

These changes have occurred despite substantial increases in the stocking rate of both cattle and elk. Between 1979 and 1994, the average number of year-round cattle increased from approximately 2,400 to 4,200 cow-calf pairs, while the number of elk increased 5-fold, from 400 to 2,000 animals. At the same time, winter hay costs have been reduced by 50%. Reproductive rates of elk average 10% greater than for elk on adjacent public lands (Squibb et al. 1991). It could be argued that this difference reflects the fact that elk on the ranch are fed supplementally during the winter. However, the same is true for elk on the nearby Hardware Ranch, administered by the Utah Division of Wildlife Resources (Kimball and Wolfe 1985).

Revenues derived from the sale of hunting permits have increased and currently account for 30-40% of annual net ranch income. Since 1983, net ranch revenues have increased by an average of approximately \$100,000 annually. The fee-hunting program, once limited to deer, now includes elk, pronghorn, moose, upland game birds, and waterfowl. Fishing and even “non-consumptive” activities such as bird watching and photography are also offered for a fee. The fact that customers continue to pay is an indicator of the willingness of wildlife enthusiasts to spend money for a high-quality outdoor experience that incorporates ethics, scenery and overall good resource management. They will understand the presence of livestock if they are informed that livestock constitute a tool that can be used to generate income while maintaining or improving the condition of the land.

Wildlife revenues support two wildlife biologists who monitor vertebrate populations and habitat condition, fund collaborative programs with the Rocky Mountain Elk Foundation, Utah State University and Utah Division of Wildlife Resources, and bolstered efforts to acquire or enhance habitats on off-ranch properties. Ranch programs have benefited migratory species like waterfowl, cutthroat trout (*Oncorhynchus clarki*) and elk that spend only part of the year on the property. State and federal agencies are routinely involved in ranch management teams and decisions that involve adjacent lands.

Several collaborative research projects have been (or are being) conducted on the DLL property. These embrace a variety of species and subject areas, including experimental investigations of some of the working assumptions underlying management of the ranch. Specific studies include those relating to sage grouse (*Centrocercus urophasianus*) ecology and management (Homer et al. 1993; Ritchie et al. 1994), foraging interactions between native ungulates and domestic livestock (Clegg 1994), ecosystem effects of herbivory (Ritchie and Wolfe 1994), and the monitoring of avifaunal communities. With respect to the latter, two breeding bird survey routes were established on the ranch in 1995.

CONCLUSIONS

The healthy condition of the Deseret Ranch, its clean water and healthy riparian areas, its abundant wildlife and profitable livestock herds have likely resulted in both an economic and aesthetic appreciation of the ranch. The positive scenario presented here occurs against the backdrop of a continuing controversy regarding the ecological effects of livestock grazing (Painter and Belsky 1993; Fleischner 1994; Savory 1988). The fact that land health has improved in the presence of grazing animals (both wild and domestic) suggests that the issue is not whether herbivores are present, but how the process of herbivory is best managed.

The economic reality of managing private lands is that they must make a profit. The Deseret Ranch has been able to maintain the integrity of its wildlands, while realizing a profit and providing wildlife recreation and livestock production. Aldo Leopold's land ethic included people; and DLL is an example of how people (employees and customers) and products can be viewed as contributing to rather than degrading land health.

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Charter of the Working Group on Sustainable Use of Ecosystem Resources of the Wildlife Society, Inc.¹

Approved By The Wildlife Society, March 25, 1995

ARTICLE I. NAME, SCOPE, AND AFFILIATION

Section 1. NAME – The name of this organization shall be the Working Group on Sustainable Use of Ecosystem Resources of The Wildlife Society, hereinafter referred to as the Working Group.

Section 2. SCOPE – This Working Group shall have as its scope of organization the assembly, study, and transfer of information relative to the conservation of wildlife through sustainable uses of ecosystem resources throughout the world.

Section 3. AFFILIATION – The Working Group shall conform to Bylaws, Code of Ethics, goals, objectives, policies, and positions adopted by The Wildlife Society, Inc. (Hereinafter, The Wildlife Society, Inc. may be referred to as The Wildlife Society or the Society.)

ARTICLE II. GOALS AND OBJECTIVES

Section 1. GOALS – Consistent with the goals of The Wildlife Society, the Working Group's goals are to:

1. Facilitate communication and the exchange of ideas and information among members of The Wildlife Society interested in wildlife conservation through sustainable use of ecosystem resources.
2. Enhance knowledge and technical capabilities of wildlife professionals and other managers of natural resources in the definition, assessment, and implementation of sustainable uses of ecosystem resources.

3. Increase public awareness and appreciation of the effects of resource uses on wildlife and of the role of sustainable resource use in wildlife management.

Section 2. OBJECTIVES – To aid in the achievement of these goals, this Working Group proposes to:

1. Provide regular communication among members of the Society interested in wildlife conservation through sustainable use of ecosystem resources, by means of meetings, symposia, workshops, newsletters, computer networks, specialty publications, etc.
2. Promote membership in The Wildlife Society to wildlife professionals interested in conservation of wildlife through sustainable use of ecosystem resources.
3. Make recommendations to The Wildlife Society Council for specific actions by the Society in the area of wildlife conservation through the sustainable use of ecosystem resources.
4. Develop draft technical reviews, position statements, and other materials in the area of wildlife conservation through sustainable use of ecosystem resources for consideration by the Society Council.
5. Provide information and technical assistance to Wildlife Society members in the area of wildlife conservation through sustainable use of ecosystem resources.
6. Provide information and technical assistance to journalists, government officials, resource managers, educators, other organizations, and the general public in the area of wildlife conservation through sustainable use of ecosystem resources.

¹Incorporated in 1948 under the laws of the District of Columbia.

ARTICLE III. MEMBERSHIP

Section 1. MEMBERS – Membership in the Sustainable Use of Ecosystem Resources Working Group shall be available to any member of The Wildlife Society with an interest in wildlife conservation through sustainable use of ecosystem resources. Working Group membership shall be available only to members of The Wildlife Society.

Section 2. DUES – Annual dues shall be payable by each Working Group member to The Wildlife Society headquarters no later than January 1. Annual dues shall not be less than \$5.00 per year and may be increased by majority vote of the Working Group members. Members who have not paid their Wildlife Society dues shall lose their membership in the Working Group. The Society shall retain a minimum of \$1.00 of the dues of each Working Group member to partially defray expenses associated with collecting dues, maintaining membership lists, providing mailing labels, and other administrative assistance. The remaining portion of each Working Group member's dues shall be distributed to the Working Group.

ARTICLE IV. ELECTIONS, OFFICERS, AND EXECUTIVE BOARD

Section 1. NOMINATIONS – The three-member Nominating and Elections Committee shall nominate a slate of two candidates for each of the elective positions, namely: Chair Elect, Secretary-Treasurer, and three additional Board Members, from the Working Group membership. When no duly elected Chair Elect exists to assume the position of Chair, two candidates for Chair also shall be nominated. Board Members will be elected at large.

Clause A. Nominees must consent to becoming a candidate.

Clause B. The slate of nominees shall be submitted to the membership at least 30 days prior to the election.

Clause C. Additional nominees may be added to the slate prepared by the Nominating and Elections Committee upon the signed support of six or more members, provided that Clause A is followed.

Clause D. A member shall not be a nominee for more than one elective position at a time and may serve in only one position at a time.

Clause E. For elective positions other than the successional positions of Chair Elect, Chair, and Past Chair, a member may be elected for up to two consecutive terms in the same elective position.

Section 2. BALLOTING – Balloting shall occur by mail and/or at the annual business meeting. Written ballots shall be received from the members and counted by the Nominating and Elections Committee. For ballot counting purposes, the Working Group Chair shall appoint a replacement for any member of the Nominating and Elections Committee who has been nominated for an elective position.

Clause A. Members in arrears shall forfeit their rights to vote during the period of their delinquency.

Clause B. A signed absentee ballot may be submitted to the Nominating and Elections Committee by a member prior to the scheduled time for counting ballots.

Clause C. The candidate receiving the largest number of votes on the written ballot shall be declared elected.

Section 3. OFFICERS – Officers of the Working Group shall consist of a Chair, Chair Elect, Secretary-Treasurer, and immediate Past Chair. Their duties are:

Clause A. CHAIR – The Chair shall have general supervisory responsibility for the Executive Board; shall preside at all meetings of the Executive Board and membership; shall appoint, with the advice of the Executive Board, chairs of all committees; and shall be an *ex officio* member of all committees, except the Nominating and Elections Committee. The Chair may represent the Working Group or appoint alternate representatives to other Working Group, Chapter, Section, or Society boards, committees, or meetings, including The Wildlife Society Council. The Chair shall be responsible for submitting an annual report of the Working Group's activity to the Society. Upon completion of a full term as

Chair, the Chair succeeds to the position of immediate Past Chair.

Clause B. CHAIR ELECT – The Chair Elect shall assume the duties of the Chair in the absence of the Chair or upon the inability of the Chair to serve and shall perform any duties assigned by the Chair. In the event the Chair Elect cannot serve in the Chair's absence, the Executive Board shall appoint a Chair, *pro tempore*. Upon completion of a full term as Chair Elect, the Chair Elect succeeds to the position of Chair.

Clause C. PAST CHAIR – The immediate Past Chair shall perform any duties assigned by the Chair.

Clause D. SECRETARY-TREASURER – The Secretary-Treasurer shall be responsible for maintaining the files, records, (Article VI, Section 4); and funds of the Working Group. Duties shall include recording the minutes of all membership and Executive Board meetings; issuing copies of the minutes to the Executive Board, members, and Society; receiving and disbursing funds; preparing and submitting an annual fiscal-year (Article VI, Section 2, Clause D) financial report to the Executive Board, members, and Society; and preparing an annual budget for approval by the Executive Board.

Section 4. BOARD MEMBERS – The three Board Members shall perform duties assigned by the Chair.

Section 5. EXECUTIVE BOARD – The Executive Board shall act as the governing body for the Working Group and shall be made up of the above named officers and Board Members (Article IV, Sections 3 and 4).

Section 6. TERM OF OFFICE – The officers and Board Members serve for approximately one year; are inducted at the Annual Meeting; assume office immediately following the Annual Meeting; and, unless reelected, terminate their duties at the conclusion of the following Annual Meeting, or at such time as their successors are elected and installed.

Section 7. VACANCIES – If the office of the Chair is vacated for any reason, the Chair Elect shall assume the duties of Chair for the balance of the

unexpired term of the Chair. All other vacancies in any unexpired term of an elective office shall be filled through appointment by the Executive Board, although an appointed Chair Elect shall serve only until the next scheduled Working Group election when the membership shall elect the next Chair. All appointees shall conform to the criteria for nominees found in Article IV, Section 1, Clauses A, D, and E.

ARTICLE V. MEETINGS

Section 1. MEMBERSHIP MEETINGS – Membership meetings shall be held at such times and places as determined and published by the Executive Board.

CLAUSE A. ANNUAL MEETING – The membership meeting held in conjunction with the Society's Annual Meeting shall be known as the Annual Meeting of the Working Group and shall be for the purposes of electing and/or inducting officers, receiving reports of officers and committees, and conducting any other business that may arise.

CLAUSE B. DUE NOTICE – Members must be notified at least 30 days prior to meetings.

CLAUSE C. QUORUM – Quorum for meetings shall be 15 percent of the membership or 15 members in good standing, whichever is less.

CLAUSE D. MEETING RULES – Order of business and parliamentary procedures at meetings shall follow *Robert's Rules of Order*, latest revision.

CLAUSE E. CHARTER – The Working Group charter shall be available for inspection during every meeting.

Section 2. EXECUTIVE BOARD MEETINGS – Executive Board meetings shall be held at such times and places as determined and published by the Executive Board.

CLAUSE A. FREQUENCY – The Executive Board shall meet at least once a year, generally in conjunction with the Annual Meeting of the Working Group, and as many additional times as necessary to conduct the business of the Working Group.

CLAUSE B. DUE NOTICE – Members of the Executive Board must be notified at least 30 days prior to meetings.

CLAUSE C. QUORUM – Quorum for meetings of the Executive Board shall be four members of the Executive Board.

CLAUSE D. MEETING RULES – Order of business and parliamentary procedures at meetings shall follow *Robert's Rules of Order*, latest revision.

CLAUSE E. CHARTER – The Working Group charter shall be available for inspection during all Executive Board meetings.

CLAUSE F. ATTENDANCE – Members are encouraged to attend Executive Board meetings, but they may not vote at such meetings.

ARTICLE VI. MANAGEMENT AND FINANCES

Section 1. EXECUTIVE BOARD – The Executive Board (Article IV, Section 5) shall govern the Working Group. The Executive Board shall conduct its affairs in conformance with the provisions of this charter, and the Bylaws of the Society. The Board is authorized to act for the Working Group between membership meetings and shall report its interim actions to the members at each succeeding membership meeting or through other communications. Any action of the Executive Board may be overridden by a two-thirds vote of the members attending a membership meeting.

Section 2. FINANCES – Funds of the Working Group shall be under the supervision of the Executive Board and shall be handled by the Secretary-Treasurer.

CLAUSE A. LIABILITY – The Treasurer need not be bonded.

CLAUSE B. SOURCE OF FUNDS – Funds shall be derived from dues, meeting fees, special activities, contributions, and other sources.

CLAUSE C. HANDLING OF FUNDS – Funds shall be placed in a federally-insured bank or savings and loan association or other money management institution/instrument approved by the Executive Board.

CLAUSE D. FISCAL YEAR – The Working Group operating and fiscal year shall begin January 1.

Section 3. REPORTS – Within 21 days of an election or other official action of the Working Group, the Secretary-Treasurer shall report such action to the Society's headquarters. The following annual reports also shall be submitted to the Society: activity (Article IV, Section 3, Clause A) and calendar-year financial (Article IV, Section 3, Clause D).

Section 4. FILES – The Working Group shall maintain files containing: Bylaws of The Wildlife Society, Charter of the Working Group, minutes of all meetings of the membership and of the Executive Board, financial statements and records, correspondence pertinent to Working Group affairs, all committee reports, and all other material designated as pertinent by the Executive Board.

ARTICLE VII. COMMITTEES

Section 1. APPOINTMENTS – The Working Group Chair shall appoint any special committees necessary to accomplish the Working Group's goals and objectives.

Section 2. REPORTS – All committee chairs shall submit a written summary of committee activities to the Working Group Chair and Secretary-Treasurer before the close of each annual meeting of the Working Group.

Section 3. ACCOUNTABILITY – All committees shall be accountable to the Executive Board and under general supervision of the Working Group Chair.

Section 4. TENURE – All committees shall serve until new committees are appointed in their stead or until the duties assigned to the committee have been discharged.

ARTICLE VIII. TECHNICAL REVIEWS, POSITION STATEMENTS, AND RESOLUTIONS

Section 1. GUIDELINES – At the request of the Society Council, the Working Group may develop

draft technical reviews and draft position statements on issues within the area of sustainable use of ecosystem resources for approval by the Society Council as the official position of The Wildlife Society. After consultation with the Society, the Working Group also may initiate draft technical reviews and draft position statements on issues within the area of sustainable use of ecosystem resources for approval by the Society Council as the official position of The Wildlife Society. The Working Group may develop resolutions on issues within the area of sustainable use of ecosystem resources for issuance as the official policy of the Working Group 1) when the content of the resolution falls within established policy of the Society, or 2) in the absence of existing policy by the Society. The Working Group shall consult with The Wildlife Society before issuing resolutions to ensure that they are not in conflict with Society policy. A copy of all Working Group resolutions shall be sent to The Wildlife Society within 21 days of approval by the Working Group. All draft technical reviews, draft position statements, and resolutions shall follow the Society's "Guidelines for Wildlife Policy Activities."

Section 2. PROCEDURES – Proposed technical reviews, position statements, and resolutions may be drafted by a special committee or individual member for consideration by the Executive Board. If approved by the Board, the statement is then submitted to the membership for a vote. Approval by a majority of the membership voting is required before the statement can be forwarded to the Society Council for approval or issued as a Working Group resolution.

ARTICLE IX. DISSOLUTION

Section 1. STANDARDS TO CONTINUE – The Working Group must continue to demonstrate its

viability to the Society's Council by meeting the following requirements: 1) filing the required annual reports (Article VI, Section 3), 2) maintaining at least 100 members, and 3) fulfilling the purposes of this charter.

Section 2. DISSOLUTION – The Society Council may dissolve the Working Group if it finds the Working Group is unable to meet the standards established in Section 1 of this Article. Upon dissolution of the Working Group, its Executive Board shall transfer all assets, accrued income, and other properties to The Wildlife Society. Said assets shall be held by the Society for five years from the date of dissolution for possible redistribution to another Working Group that may form to replace it. If another Working Group on Sustainable Use of Ecosystem Resources is not established within the five-year period, the Society may use or distribute all assets, accrued income, and other properties in any manner consistent with Society bylaws.

ARTICLE X. AMENDMENT TO CHARTER

Section 1. PROCEDURE – This charter may be altered or amended by a majority of the Working Group members voting by mail ballot or at any membership meeting provided due notice of the proposed changes (Article V, Section 1, Clause B) has been provided. A member who will be absent from the meeting may file an absentee ballot (Article IV, Section 2, Clause B).

Section 2. CONFORMANCE – No amendment to this charter shall be enacted that results in a conflict with The Wildlife Society Bylaws. Amendments to this charter that are approved by the Working Group's membership, as defined in Section 1 of this Article, do not become effective until approved by the Society.



Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota

*Station Headquarters: 240 W. Prospect Rd., Fort Collins, CO 80526

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